

SYSTEMATICS AND GEOGRAPHIC HISTORY OF THE GENUS
PYRGUS IN THE PALAEARCTIC REGION
(LEPIDOPTERA, HESPERIIDAE)

by

R. DE JONG

Rijksmuseum van Natuurlijke Historie, Leiden

ABSTRACT

A systematic and zoogeographic study on the Palearctic species of the genus *Pyrgus*, comprising a taxonomic review, a description of the geographic variation and a reconstruction of the geographic history. Some zoogeographic problems are discussed and the *Pyrgus* species are classified as faunal types.

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1. INTRODUCTION

1.a. Scope

The present study is an attempt to reconstruct the geographic and, in a few cases, the evolutionary history of the Palaearctic species of the genus *Pyrgus*, on the basis of their recent ranges and geographic variation patterns. The author believes that the high morphologic and ecologic diversity of *Pyrgus* can be understood as, at least partially, the result of geographic isolation and subsequent differentiation of former geographically connected populations.

The history of *Pyrgus*, reconstructed in this way, clearly shows the enormous impact of the alternation of Glacial and Interglacial Periods during the Pleistocene, on the distribution and differentiation of the members of *Pyrgus*. Details of the history, however, are often vague.

The history of *Pyrgus* is discussed in relation to the general history of the Palaearctic fauna. This leads towards a zoogeographic classification of the *Pyrgus* species into faunal types; a comparison is made with a classification into distributional types.

As taxonomic research must provide the basic facts for the reconstruction of the history, only taxonomically well-known groups can be selected for a historic-zoogeographic study. The Palaearctic members of the genus *Pyrgus* are such a group. This is mainly due to the work of Rambur (1837-1842), who discovered the great importance of the male genitalia for the identification of the species, of Reverdin (from 1910 onwards), of Warren (1926, 1953) and of Evans (1949). Moreover, Alberti, Kauffmann, Opheim, Picard, and others have contributed to our knowledge, in dealing with detail problems. Nevertheless, there still exists much disagreement about the taxonomy of *Pyrgus*, especially with regard to the delimitation of species and subspecies. Therefore, it was necessary to review the taxonomy of *Pyrgus*, before a zoogeographic study of the genus could be made. It must be emphasized, however, that this review is not the aim of the present study, but only a means to permit a reconstruction of the geographic and evolutionary history of this interesting group, which has fascinated the author for many years.

1.b. Taxonomic categories

The influence of the application of the biological species concept on the number of species within the genus *Pyrgus* in the Palaearctic becomes apparent, when we compare the 32 species recognized by Warren (1926) on the base of a typological species concept, with the 19 species recognized by Evans (1949) who accepted a biological approach. The typological and biological species concepts have extensively been discussed by Mayr (1942, 1963). It would suffice here to refer to these publications, if there were not many authors who in recent times have still applied a typological species concept in entomology. Three examples concerning Hesperidae are:

(a) Heydemann (1954: 426): "*Carcharodus* Hb. *swinhoei* Watson ist gute Art und von der äusserlich ausserordentlich ähnlichen *frutillarius* Poda (= *alceae* Esp.) durch verschiedenen Genitalapparat des Männchens getrennt".

(b) Warren (1957: 375), having examined the female genitalia of the N. American *Pyrgus freija* and the Scandinavian *Pyrgus centaureae*, concludes: "These mounts proved

beyond doubt that *P. freija* and *P. centaureae* were distinct species, . . ."

(c) Sichel (1962) concluded from morphologic, chorologic and palaeo-zoogeographic data that *Pyrgus malvae*, *P. malvoides*, *P. melotis* and *P. ponticus* were distinct species. Palaeo-zoogeographic data can never prove conspecificity, nor the reverse; morphologic data, on the other hand, sometimes can, in combination with chorologic data, viz. when the study concerns contact zones of morphologically different forms. Sichel only showed that there are morphologic differences between the four forms just mentioned and that these forms are allopatric.

In these and in many other cases, morphologic differences between specimens and not non-interbreeding of populations are considered decisive for specific distinction. As long as the typological species concept will be applied, there will be much disagreement about classification. It may be useful to quote here the definition of the (biological) species of Mayr (1942: 120): "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." This concept will be adhered to in the present study.

The dynamic character of the species is apparent in those cases where neighbouring populations interbreed only to a limited extent, showing that these populations have attained a certain degree of specificity with regard to each other. Such cases are by no means rare; in *Pyrgus* strikingly limited interbreeding is known in groups which in the present work have been called superspecies *malvae*, superspecies *carlinae* and the *alveus* species complex. It does not seem relevant to the author at what percentage of hybrids we can consider the populations, which come into contact with each other, specifically distinct. In the superspecies *malvae* and *carlinae* I term the component species, which are only partially reproductively isolated, semispecies (see Lorkovic, 1953; Mayr, 1963, 1969). Further research in the *alveus* species complex may make it preferable to apply the term semispecies to what has been called here *accretus* subspecies group and to *P. warrenensis* (see also Chapter 2).

The term semispecies was proposed by Mayr for the designation of the component species of a superspecies (see Mayr, 1963). Mayr (1969: 52) defined the superspecies as follows: "A superspecies is a monophyletic group of closely related and largely or entirely allopatric species". By broadening the term semispecies in order to include all border-line cases in speciation (see Mayr, l.c.) it may be useful to broaden also the term superspecies, to include not only semispecies which are entirely reproductively isolated, but also semispecies which are partially reproductively isolated. In this sense I apply the term superspecies, to *malvae* and *carlinae*. By extending the term superspecies, it becomes clear that in specific cases there is not an essential difference between species and superspecies, but only a difference in degree of speciation.

Similarly, superspecies and species groups do not differ essentially but only in degree of distributional overlap. The present author prefers to use the term species group instead of the term subgenus, as the former has no nomenclatural consequences. In some cases it may have practical value to unite species groups into a subgenus, e.g. the subgenus *Scelotrix* of *Pyrgus*. The advantage of recognizing a subgenus for a single superspecies, as subgenus *Pyrgus* for superspecies *malvae*, is at least disputable. Of course, any decision with regard to the problem "genus versus subgenus" is entirely subjective. This applies also to the problem "subgenus versus species group" and even "genus versus species group".

Lepidopterists are notorious for their treatment of infraspecific variation. The immense

number of names for all kinds of variations has little contributed to the understanding of the variation. Only the geographic variation is important for the present study. The treatment of this geographic variation by various authors does not always show a clear understanding of the subject. Most, if not all, difficulties arise from different views (if there is any view at all) about the subspecies concept. Some authors apply the term subspecies to any geographic variation, hereditary or not; others confuse subspecies with the occurrence of certain characters and describe then even sympatric "subspecies" of the same species. Kauffmann (1951) succeeded in combining both not current conceptions of the term subspecies. He observed e.g. that the "subspecies" *caecus* and *serratulae* of *Pyrgus serratulae* fly together in Switzerland and that the ratio between them changed annually and depended on weather conditions. The extensive literature concerning the subspecies (apparently overlooked by many lepidopterists) makes further extensive discussion of the problems here senseless; it may suffice to refer to Mayr (1969) for a recent treatment of the subject and for many references. Mayr (l.c.: 41) defined the subspecies as follows: "A subspecies is an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of the species."

We should be aware of the fact that this definition may easily lead to the recognition of subspecies which are evidently taxonomic artifacts and therefore of no use in taxonomy. For example, Mayr (1963: 349) states: "Nor should the subspecies be confused with phenomena of a very different nature, such as character gradients (clines)." However, his definition is not at all a guarantee against a confusion. Furthermore, misunderstanding of Mayr's definition could easily lead to the recognition of nongenetic ecophenotypic varieties as subspecies. For example, a common nongenetic ecophenotypic variation in *Pyrgus* at high altitudes concerns the reduction of white spots on the upper-side of the wings. Most specimens of *P. serratulae* in the Alps at altitudes above 2000 m have very small spots; they are known under the name "forma *caecus*". Evidently, the recognition of a "subspecies" *caecus* is of no use in taxonomy, as this "subspecies" would be a taxonomic artifact.

Virtually Mayr's subspecies concept would be entirely typological, if it were not based on a biological species concept. Mayr has never stated that a subspecies has to be phenotypically uniform under all conditions, but I am of the opinion that especially the typological concept has caused many difficulties. If we abandon a typological idea altogether and admit that a subspecies is not only a taxonomic but also a zoogeographic concept, it seems possible to avoid any confusion and to define a subspecies representing a natural unit, as follows:

A subspecies is an, at present or formerly, geographically isolated group of populations of a species, which can be distinguished by one or more characters from other such groups of populations of the species.

The existence of such subspecies can be concluded from the idea of speciation through geographic isolation. The subspecies thus defined is a useful tool for a historic-zoogeographic study. The fact that it is often very difficult to recognize a subspecies, cannot be a serious objection. However, we must be aware that not all geographically isolated populations differentiate into recognizable subspecies (for example, see Chapter 3, *P. andromedae*). For the subjective nature of the decision whether a geographic isolate differs sufficiently from other populations to warrant subspecific separation, see Mayr (l.c.). Some attention will be paid to the question, how groups of populations,

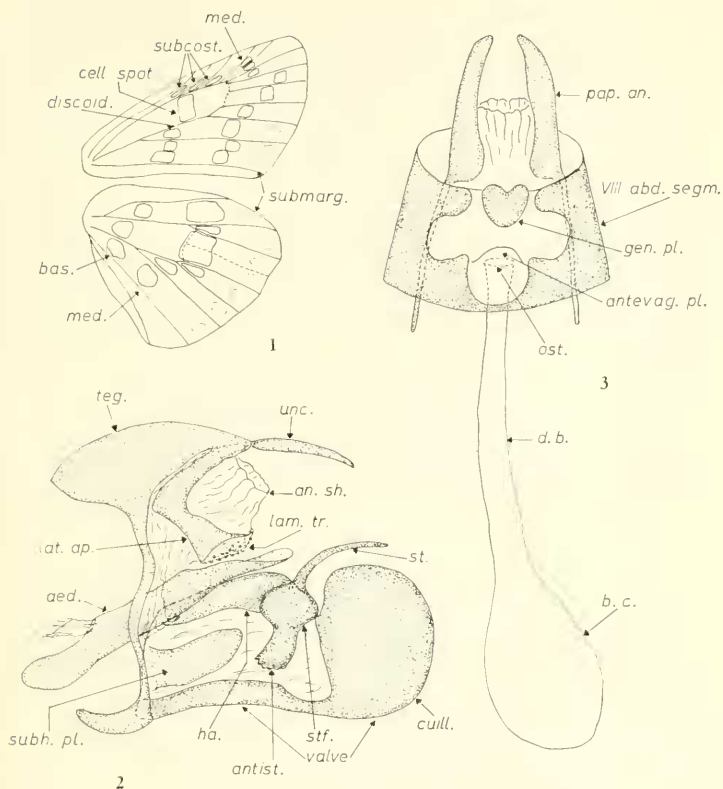


Fig. 1—3. Wing markings, male and female genital armatures in *Pyrgus*. 1. Wing markings: bas. = basal spots; discoid. = discoidal series; med. = median series; subcost. = subcostal spots; submarg. = submarginal series. 2. Male genital armature, lateral view, with left valve removed: aed. = aedeagus; an. sh. = anal sheath; antist. = antistyle; cuill. = cuiller; ha. = harpe; lam. tr. = lamina transversa; lat. ap. = lateral apophyses; st. = style; stf. = styli; subh. pl. = subharpal plate; teg. = tegumen; unc. = uncus. 3. Female genital armature, ventral view: antevag. pl. = antevaginal plate; b.c. = bursa copulatrix; d.b. = ductus bursae; gen. pl. = genital plate; ost. = ostium; pap. an. = papilla analis; VIII abd. segm. = eighth abdominal segment

which were formerly geographically isolated, can be recognized. This can only be done by tracing the existence of zones of secondary intergradation. Of course, our decision whether an intergradation zone is primary or secondary, may be incorrect, but this is not due to an artificial subspecies concept, but to a wrong interpretation of the facts. A discussion on zones of intergradation can be found in Mayr (1963: 368-384).

The subspecies thus recognized may be very variable, even geographically. Undoubtedly, this geographic variation within the subspecies is partly clinal, partly ecophenotypic (as defined by Mayr, 1969: 402): "A nongenetic modification of the phenotype by specific ecological conditions, particularly those of a habitat."). It has often been emphasized that it is undesirable to give scientific names to these variations. Only the most striking ones of the described forms have been mentioned in this paper (as "forma"). Due to lack of material or data it is at the moment often impossible to decide whether a variation is ecophenotypic or clinal. In the present study I am attempting to separate subspecific, clinal and ecophenotypic variations. I am aware of the fact that the results will not always be convincing, but recognition of these types of variation may be a stimulus to fill the many gaps in our knowledge.

1.c. Wing markings and genital armature

In the present paper a combination has been adopted of the terms used by Warren (1926) and Evans (1949) to denominate the wing markings and the various parts of the male genitalia. For the female genitalia I have followed Opheim (1956) and Guillaumin (1966).

(a) Wing markings (Fig. 1).

Fore wings — from termen to base there are three series of spots: a submarginal, a median, and a discoidal series. In addition, there are subcostal spots, a cell spot (in the cell) and a discal spot (closing the cell). The separate spots are indicated by their intervenal space, e.g. median spot in space 6, submarginal spot in space 2, etc. (for the numbering of the veins and the intervenal spaces, see Evans, 1949). The submarginal spots are often absent or vague.

Hind wings — from termen to base there are three series of spots: a submarginal, a median, and a basal series. The separate spots are numbered as on the fore wings. The median spots in spaces 4 and 5 are confluent and indicated as the central spot. The spots on the upperside of the hind wing are often very faint.

(b) Male genitalia: Fig. 2.

(c) Female genitalia: Fig. 3.

The bursa copulatrix lacks a signum, a structure often important as a diagnostic, specific character in other groups of Lepidoptera.

1.d. Nomenclature

Little attention has been drawn to matters of nomenclature and it has not been attempted to list all names relating to *Pyrgus* and its species. A full account of these names can be found in Evans (1949). Names proposed after 1949 have only been included here when they refer to species or subspecies or when they relate to forms which I think to be worth mentioning.

In one respect I have intentionally neglected the International Code of Zoological

Nomenclature, viz. by omitting the parentheses enclosing the author's name in new combinations, as meant in Article 51d of the Code. The use of parentheses does not add necessary, important or even interesting information. It only indicates that the author of the species-group name (in nomenclatural sense) listed the taxon represented by this name in another genus, as can be expected when names are rather old. If one wishes to use parentheses, the names of the authors of all specific and most subspecific names of *Pyrgus* can be enclosed in parentheses.

1.e. Material

The material examined for this study comprises more than 10.000 specimens. Though this number does not appear very small, much more material is needed to solve some of the taxonomic problems. I must, however, stress the fact that many problems can only be solved by a study on the spot and not by examining large numbers of specimens in collections. In the present work such problems are apparent a.o. in the *alveus* species complex and the superspecies *malvae*.

Special mention must be made of the large collections of HesperIIDae in the British Museum (Natural History). These collections, containing e.g. the very important Ch. Oberthür collection, have been arranged by the great specialist of HesperIIDae, the late Brigadier W. H. Evans, whose extensive work on the HesperIIDae of the world was based on this material. I am glad to have had the opportunity of examining this material during a visit to the British Museum in the spring of 1971.

1.f. Acknowledgements

For the loan and gifts of material, for valuable information and for help in various ways I am greatly indebted to the following persons and institutions: Dr. B. Alberti (Waren-MüritZ, DDR) (abbreviated: BA), G. Bernardi (Muséum National d'Histoire Naturelle, Paris) (MP), F. Bink (Amsterdam), H. Coene (Amsterdam) (HC), Dr. W. Forster (Zoologische Sammlung des Bayerischen Staates, Munich) (ZSM), M. Guillaumin (Paris) (MG), Dr. H. J. Hannemann (Zoologisches Museum der Humboldt-Universität, Berlin) (ZMHB), F. C. Howarth (British Museum, Natural History, London) (BM), Instituut voor Taxonomische Zoologie (Zoölogisch Museum, Amsterdam) (ZMA), Dr. F. Kasy (Naturhistorisches Museum, Vienna) (MW), A. Lillehammer (Zoologisk Museum, Oslo) (MO), J. H. Lourens (Amsterdam), Dr. E. Niculescu (Bucuresti), M. Opheim (Oslo), H. van Oorscot (Amsterdam) (HO), R. van Oorscot (Amsterdam), Rijksmuseum van Natuurlijke Historie (Leiden) (ML, RJ), Mrs. M. A. da Silva Cruz (Candal-Gaya, Portugal), H. Stammeshaus (Amsterdam) (HS), J. Thurner (Klagenfurt, Austria), B. C. S. Warren (Folkestone, England), J. Wolschrijn (Muiderberg, Netherlands), C. W. Wyatt (Farnham, England) (CW).

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There is one person who has helped me more than I can realize at the present or than she will ever admit: I am profoundly grateful to my wife.

1.g. Methods, measurements and abbreviations

(1). There are various methods of measuring the size of a butterfly, from such a vague term as "wing span" to the exact but rather odd method of Warren (1926) of measuring the length from the centre of the thorax to the tip of the wing and multiplying it by two. I have applied a simple but exact method by measuring the length of the fore wing from base to apex (without fringes). Thus all measurements given in this paper refer to the length of the fore wing.

(2). To avoid confusion between specific and subspecific names, a species (and semispecies) is indicated by the combination *Pyrgus a-us* or *P. a-us*, a subspecies by the combination *a-us b-us* or ssp. *b-us*, whatever may be appropriate. Names referring to the infrasubspecific variation can be recognized by the word "forma" or the abbreviation "f." preceding the name of the variety.

(3). In the drawings of the male genitalia the aedeagus and the left valve have been omitted or only the right valve has been pictured.

The drawings of the female genitalia only show the ventral side of the eighth abdominal segment.

(4). Much care has been given to the drawing of the distribution maps; their scale, however, does not permit the reproduction of small disjunctions. The maps serve to facilitate a rapid recognition of a particular distributional area and a rapid comparison of different distributional areas.

Although as many as possible faunal lists have been examined (the most important ones have been listed in Chapter 7), it must be stressed that the distribution limits, especially in Asia, are often very poorly known.

Abbreviations used

f.	=	forma	upf	=	upperside of fore wing
ssp.	=	subspecies	uph	=	upperside of hind wing
			unf	=	underside of fore wing
			unh	=	underside of hind wing

2. THE GENUS *Pyrgus* HÜBNER, 1819

2.a. Delimitation

The delimitation of the genus *Pyrgus* accepted in this study is that proposed by Warren (1926) (under the name *Hesperia*). This delimitation has been generally accepted, but in recent times some authors (e.g. Alberti, 1969), have used the name *Hesperia* again in the sense of most authors prior to Warren, i.e., to include also the species which have been classified by Evans (1949) in the genera *Spialia* and *Muschampia* (recte *Syrichthus*, see Hemming, 1967). Therefore, it may be useful to summarize the distinctive characters of *Pyrgus* and to call attention to a few, hitherto overlooked. The type species of *Hesperia* Fabricius, 1793, *H. comma* Linnaeus, and the type species of *Pyrgus* Hübner, 1819, *P. malvae* Linnaeus, are usually regarded as non-congeneric (they are classified in different subfamilies). Therefore, the use of the name *Hesperia* instead of *Pyrgus*, should be avoided (see Hemming, 1934a).

The characters of *Pyrgus* mentioned below refer to Palearctic species only. Most (and perhaps all) American *Pyrgus* species share these characters, but for the delimitation in America (only interesting with regard to the genus *Heliopetes*) I may refer to Evans (1935). *Pyrgus* may be characterized as follows.

Fore wing median spots in spaces 4 and 5 completely detached from the median spots in spaces 6 to 8, nearer the termen; submarginal spots absent or faint and incomplete.

Male hind tibiae with a hair tuft fitting into a double thoracic pouch.

Male fore wing with a costal fold, enclosing specialized, androconial scales (absent in superspecies *alpinus*). The fact that the androconial scales offer a distinctive character seems to have been overlooked. These scales are more or less fusiform, very narrow, hair-like at the apex (Fig. 4-6). The variation in width ($6.9\ \mu$) and in length ($180\text{--}300\ \mu$) does not seem to be of great specific value, as there exists much overlap in the

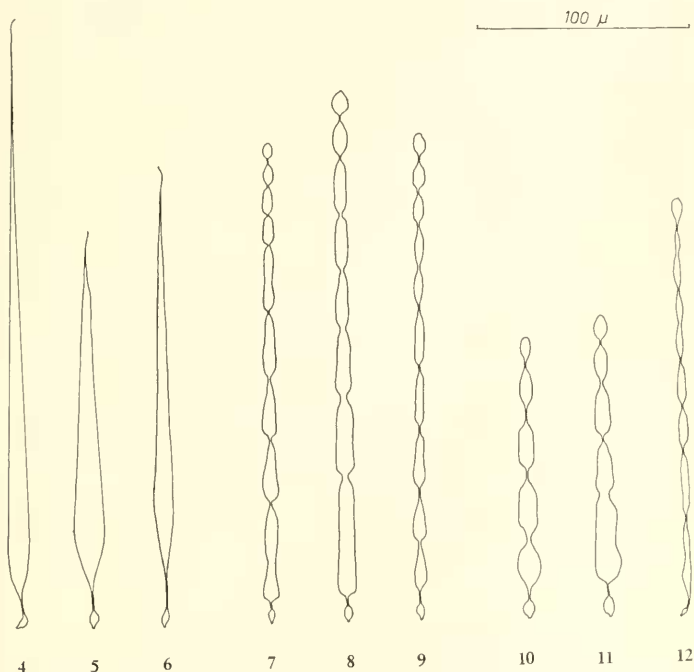


Fig. 4—12. Androconial scales in *Pyrgus*, *Carcharodus* and *Syrichtus*. 4, *Pyrgus sidae* (Turkey); 5, *P. andromedae* (Abisko, Sweden); 6, *P. alveus* (Bavaria); 7, *Carcharodus alceae* (Tarragona, Spain); 8, *C. boeticus* (C Spain); 9, *C. floccifer* (Italian Alps); 10, *Syrichtus proto* (Marash, Turkey); 11, *S. tessellum* (Aksu, C Asia); 12, *S. cribrillum* (N Tibet)

various species. *P. sidae* stands somewhat apart by its very long androconial scales: 280-300 μ , in the other species the length varies mainly between 180-220 μ .

Male genitalia with well-defined, strongly sclerotized, highly specialized lateral apophyses. In the Palaearctic species the distal end of the harpe is differentiated into a style, a styliifer and an antistyle.

Female genitalia have not been used in the search for distinctive generic characters in Hesperiiidae. I wish to call attention to a character which does not concern the genitalia proper, but the general sclerotization of the eighth abdominal segment. In *Pyrgus* this sclerotization consists of a single part of variable shape at both sides of the segment. The left-hand and right-hand sclerites are connected ventrally and dorsally by a membrane; in some species the sclerites are connected ventrally, by a narrow sclerotized band.

By these characters *Pyrgus* stands taxonomically somewhat apart. The genera supposed to be most closely related to *Pyrgus*, viz. *Carcharodus*, *Syrichtus*, and *Spialia* (cf. Evans, 1949, 1953), have more characters in common with each other (particularly *Carcharodus* and *Syrichtus*) than with *Pyrgus*. The fact that there is some disagreement about the classification of *Carcharodus* and *Syrichtus*, does not need to bother us here. On the fore wing the median spots in spaces 4 and 5 (if present) are contiguous to the median spots in spaces 6 to 8 in *Syrichtus* and *Spialia*. The median spots in spaces 4 and 5 are absent in *Carcharodus*, but very rarely a minute spot is visible in space 5; this spot is contiguous to the median spots in spaces 6 to 8.

A hair pencil on the hind tibia of the males is wanting in *Carcharodus*, *Syrichtus* and *Spialia*. A costal fold is present in the males of *Carcharodus* and *Syrichtus* (except *S. antonia*) and of a few Ethiopian species of *Spialia*.

In *Carcharodus* and *Syrichtus* the costal fold encloses androconial scales which are quite different from the type found in *Pyrgus*: they are constricted at varying intervals (Fig. 7-12). I did not examine the androconial scales in *Spialia*.

In the male genitalia the lateral apophyses are absent or rather well-developed (in some species of *Syrichtus* and *Spialia*); they are less specialized than in *Pyrgus*. The distal end of the harpe is very variable, but never with a style.

The sclerotization of the eighth abdominal segment in the females usually consists of two sclerites on both sides, the four parts connected by a membrane. In some *Spialia* species (e.g. *S. sertorius*) there is a single sclerite on both sides, dorsally connected by a membrane, ventrally by a narrow band of continuous sclerotization.

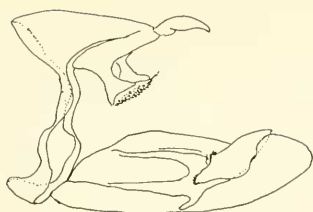
In conclusion, it appears highly undesirable to consider the species of the genera *Syrichtus*, *Spialia* and *Pyrgus* congeneric.

2.b. Classification

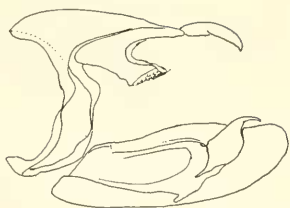
One of the characters of the genus *Pyrgus* is the strong sclerotization of the lateral apophyses. Their specialized nature makes these structures very useful for the classification of the genus.

The classification of the genus by Warren (1926) is mainly based on the development of the lateral apophyses:

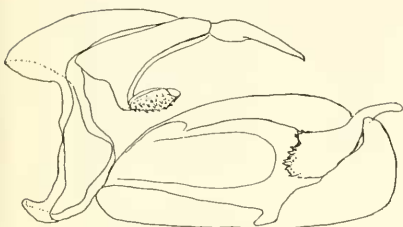
Subgenus *Teleomorpha* — lateral apophyses ventrally broadly connected.



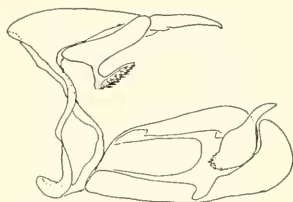
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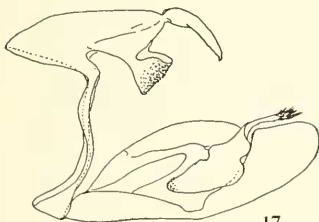
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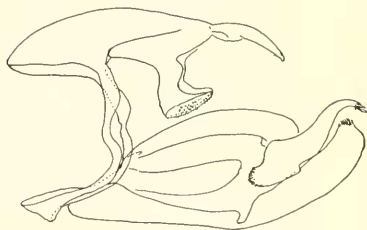
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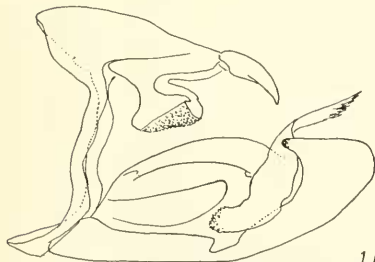
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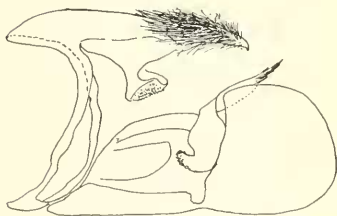
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18



19



20

1 mm

Fig. 13—20. Male genitalia. 13, *Pyrgus maculatus* (Amdo); 14, *P. bieti* (Ta Tsien Lou); 15, *P. oberthuri* (Ta Tsien Lou); 16, *P. dejeani* (Nan-Shan); 17, *P. alpinus* (C Asia); 18, *P. carthami* (Digne, SE France); 19, *P. sidae* (Aksehir, Turkey); 20, *P. badachschanus* (Panjshir V., Hindu-Kush)

Subgenus *Hemiteleomorpha* — lateral apophyses with a narrow ventral connection.

Subgenus *Ateleomorpha* — lateral apophyses ventrally not connected.

The name *Teleomorpha* is a junior objective synonym of *Scelotrix* Rambur, 1857, and the name *Hemiteleomorpha* is a junior objective synonym of *Pyrgus* Hübner, 1819; see Hemming (1967).

This classification has generally been accepted, but Guillaumin (1966) stated that the structure of the female genitalia does not support (nor contradict) this concept (he only dealt with the species of France). This statement is only partly true and apart from this I do not see why it should devalue the classification. There is no obvious reason to assume that the male and female genitalia evolved at the same speed.

Because of the large number of species it is practical to divide the genus into subgenera. However, any biological meaning disappears when the division is artificial, in other words: when the subgenera are not monophyletic. Of the three subgenera proposed by Warren, *Scelotrix* and *Pyrgus* can be considered monophyletic. The latter comprises only one superspecies (*malvae*); at least two of the four species recognized by Warren in this subgenus interbreed to some extent (*malvae* and *malvoides*). In the subgenus *Scelotrix* the presence in all species of the ventral connection of the lateral apophyses and of the structure of the genital plate can only be attributed to an evolution from a common ancestral situation.

The common feature of the species of Warren's subgenus *Ateleomorpha* is the absence of a ventral connection of the lateral apophyses. The absence of a structure is much more difficult to interpret phylogenetically than its presence. Besides, there is much variation in the shape of the lateral apophyses and this variation runs to some extent parallel to that found in the female genitalia, in the sense that in the species that have most similar male genitalia, also the female genitalia are most alike. Although it is not impossible that the species united by Warren into the subgenus *Ateleomorpha* are monophyletic, I believe the conception of monophyly in this case to be less well-founded than in the subgenus *Scelotrix*. Therefore, I prefer to restrict the subgeneric distinction to the species of the *alveus* and *cinarae* groups of Warren, thus excluding *P. serratulae* and *P. onopordi* and the superspecies *carlinae* (comprising the species *carlinae* and *fritillum* = *cirsii*, recognized by Warren) which I prefer to consider species of uncertain affinity (in relation to each other and to other species). However, the type species of *Ateleomorpha* is *P. onopordi* (Hemming, 1934); therefore this name cannot be used as a subgeneric name for the *alveus* and *cinarae* groups. As I have no intention of proposing new names in this paper I am referring to the *alveus* and *cinarae* groups as "the *alveus* species complex".

Subgenus *Scelotrix*

Male genitalia. — Lateral apophyses connected ventrally by a broad, spined, sclerotized plate. Sichel (1962) named the narrow plate in the subgenus *Pyrgus*, lamina transversa; this name can also very well be used in the subgenus *Scelotrix*. Uncus short, more or less curved, usually with a blunt apex.

Female genitalia — An obvious genital plate, free (not embedded in a membrane), variable in size, usually heart-shaped and always with an incision at the top. In the sclerotized or membranous sternum of the eighth abdominal segment there is a corrugant sclerotization in most species.

Facies — Median spot 5 unh usually projecting towards the base of the wing. In

some species a pale spot at the base of space 2 upf, always absent in members of the other Palearctic subgenera, but present in all American species (see below).

For the division into species I have followed Evans (1949), except in the case of *alpinus* which was given specific rank by that author, but which I consider a super-species (for reasons, see Chapter 3).

Some species resemble each other so closely with regard of the male and sometimes also of the female genitalia, that we may assume a close relationship. This is the case in the following species.

P. maculatus and *P. bieti* resemble each other by the shape of the valvae, the indistinct subharpal plate, the formation of style and antistyle, the uncus, the lateral apophyses and the aedeagus (Fig. 13 and 14). It should be noted that the unh of *P. maculatus* deviates from all known species of *Pyrgus*.

P. oberthuri and *P. dejeani* resemble each other particularly by the strong dorsal development of the lateral apophyses, the uncus, the aedeagus and the general formation of the valvae (Fig. 15 and 16). Externally they are also very similar, but so is the case with many *Pyrgus* species.

P. alpinus, *P. cashmirensis* and *P. darwazicus*. The male genitalia are almost alike, although the species differ very obviously in pattern (see Chapter 3 and Fig. 17, 58-60). A further common feature is the absence of a costal fold in the males, a unique character in the Palearctic *Pyrgus* species. I unite these species in a superspecies.

P. andromedae, *P. cacliae*, and *P. centaureae*. The male genitalia differ mainly in the shape of the cuiller and of the antistyle (Fig. 51-56). The female genitalia chiefly differ in the corrugant sclerotization of the sternum of the eighth abdominal segment, but, as is shown in Fig. 21-29, the difference between these species is less than that from other species.

The other species of the subgenus (*P. carthami*, *P. sidae* and *P. badachschanus*) seem to stand more apart, or at least, their relationship to other species (and to each other) is rather obscure.

The little developed cuiller and style-antistyle of *P. carthami* (Fig. 18) suggest a relationship with the Chinese species (*P. maculatus*, *P. bieti*, *P. oberthuri*, *P. dejeani*). The development of the sternum of the eighth abdominal segment in the female (Fig. 27) supports this, although the genital plate is larger. Externally *P. carthami* is not at all related to Chinese species, but more related to the European species; however, most *Pyrgus* species look very much alike.

Warren (1926) thought *P. sidae* closely related to the species *P. centaureae* and *P. alpinus*, but he only examined the male genitalia (Fig. 19) and even then the relationship is debatable; as to the female genitalia (Fig. 28), *P. sidae* does not closely resemble any other species and the same applies to the colour and design unh (alternating white and orange bands).

Special mention must be made of *P. badachschanus*. This species, confined to N Afghanistan, does not resemble any other *Scelotrix* species with regard to the male genitalia (Fig. 20). The extremely dense hairing of the uncus is a unique character and the very large cuiller only recalls the structure found in the *alvens* species complex. As far as I know, the female genitalia have remained unknown, but I could examine a female from the captures made by Wyatt & Omoto (1966) (Fig. 29). Although clearly of the *Scelotrix* type, it lacks the corrugant sclerotization of the sternum of the eighth abdominal segment.

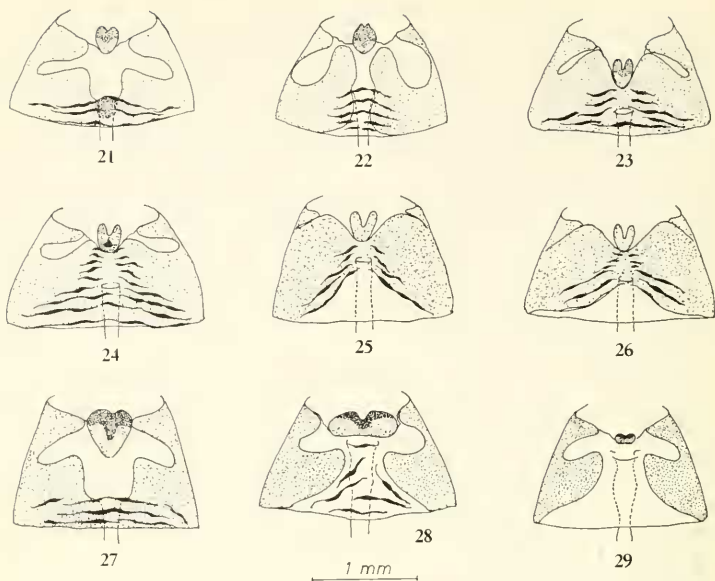


Fig. 21—29. Female genitalia. 21, *Pyrgus maculatus* (Amur); 22, *P. alpinus* (Fort Naryn, C Asia); 23, *P. andromedæ* (Abisko, Sweden); 24, *P. cacaliae* (Swiss Alps); 25—26, *P. centaureae* (Lapland); 27, *P. carthami* (Pyrenees); 28, *P. sidae* (Aksehir, Turkey); 29, *P. badachschanus* (Panjshir V., Hindu-Kush)

Subgenus *Pyrgus*

Male genitalia. — Lateral apophyses ventrally connected by a narrow, either spined or unspined lamina transversa. The main difference with the subgenus *Scelotrix*, apart from the narrowness of the lamina transversa, is the development of small to very large processes of the lateral apophyses. Uncus short, entire, incised or longitudinally split into two parts, the strongly sclerotized apex rather blunt.

Female genitalia. — Genital plate very large, entire or split into two parts. No corrugant sclerotization.

Facies. — Above spots usually well-developed, even the submarginal spots uph; unh spots reduced, median spot 5 usually more or less projecting towards the base of the wing.

There are three types of genitalia (Fig. 30-35).

The *malvae* type. — Uncus bipartite; lamina transversa spined; lateral apophyses with long, strongly spined processes; cuiller pointed; style-antistyle short and broad. Genital plate bipartite.

The *melotis* type. — Uncus entire or partly bipartite; lamina transversa smooth,

laterally with a spine; lateral apophyses with long, unspined processes; cuiller rounded; style-antistyle slender. Genital plate entire, but apically incised.

The *malvoides* type. — Uncus narrow, entire, usually apically more or less incised; lamina transversa smooth; short spined processes comparable with the long processes in the *melotis* and *malvae* types, but much less developed; valvae resembling the *melotis* type. Genital plate entire, apically incised as the *melotis* type.

Presumably this subgenus comprises the most discussed forms of HesperIIDae. Warren (1926) recognized four allopatric species in this subgenus: *malvae*, *malvoides*, *melotis* and *ponticus*. Picard (1948-a, 1950-a) demonstrated the occurrence of hybridization between *malvae* and *malvoides* in C. France. Hybridization was also reported from N Tyrol (Kauffmann, 1955) and from Triest (Alberti, 1956). However, in Switzerland, where *malvae* occurs in the north and *malvoides* in the south, hybridization has not been reported (Kauffmann, 1951). The two forms are possibly geographically separated by a very narrow zone (Wiltshire & de Bros, 1966).

The situation in C France has been re-examined by Guillaumin (1962), who found a lower rate of hybridization than stated by Picard; like Picard he did not mention a percentage of hybrid specimens, but at least the hybridization seems to occur more than occasionally.

For the evaluation of the hybridization it is useful to mention the fact that *malvae* is usually monovoltine and *malvoides* bivoltine.

In France the single generation of *malvae* flies from the end of April until the beginning of June and the first generation of *malvoides* from the middle of May until the middle of June (Guillaumin, 1964). Thus, only late specimens of *malvae* and early specimens of *malvoides* have a chance to interbreed. Besides, in Switzerland *malvae* and *malvoides* may differ in habitat preference, *malvae* being commoner in the valleys and *malvoides* in the mountains (Wiltshire & de Bros, 1966).

The situation can be summarized as follows. The allopatric forms *malvae* and *malvoides* interbreed where they come into contact. The proportion of hybrids depends on the flight period and habitat preference of both forms and is, therefore, locally different.

The absence of transitional populations between *malvae* and *malvoides* has led to various theoretical reflections (e.g. Pröse, 1955a; Sichel, 1962a; Niculescu, 1967). Generally the two forms are considered to be separate species or at least semispecies of a superspecies. Only Evans (1949) united them as subspecies (together with *melotis* and *ponticus*) into a single species. I fail to see why the choice of a term for a particular situation would be so important, that much time and trouble is spent in order to show, on merely theoretical grounds, that other authors have used a wrong term for this, instead of recognizing the fact that the situation is much more important than attaching a name to it. Therefore the remark of Guillaumin (1970, in litt.), that after a study of many years of the situation in France, he cannot say whether *malvae* and *malvoides* are species or subspecies, is much more important. It shows that in this case the decision "species against subspecies" should be justified by practice and cannot be evaluated theoretically. As both *malvae* and *malvoides* can be subdivided into subspecies it seems convenient to call them semispecies of a single superspecies. As hybridization seems to occur more than occasionally, at least in France, I do not see a practical value in declaring them species as this would obscure the situation.

The *melotis* type of genitalia is found in the externally different forms *melotis* and *ponticus*. Unlike Sichel (1962) I could not find constant differences of the male

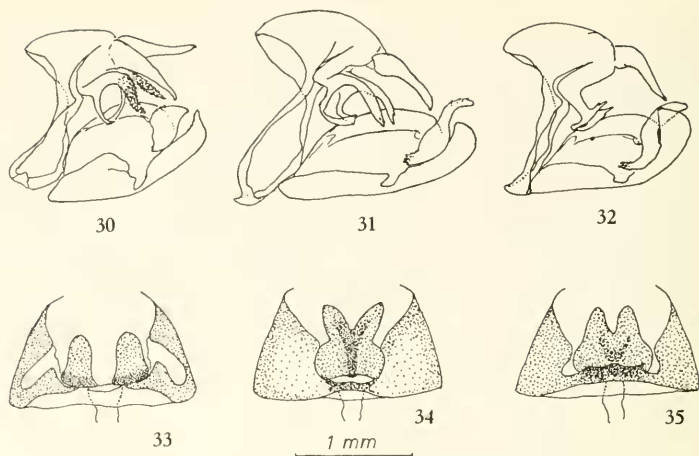


Fig. 30—32. Male genitalia. 30, *Pyrgus malvae malvae* (Netherlands); 31, *P. melotis ponticus* (Aksehir, Turkey); 32, *P. malvoides malvoides* (Pyrenees). Fig. 33—35. Female genitalia. 33, *P. malvae malvae* (Netherlands); 34, *P. melotis ponticus* (Aksehir, Turkey); 35, *P. malvoides malvoides* (Pyrenees)

genitalia in *melotis* as against those in *ponticus* and as they also intergrade externally more or less I do not see any reason for considering them specifically distinct (see further Chapter 3). The zone of contact between *malvae* and *ponticus* is presumably situated in the west of Turkey, but at least as far to the west as Aksehir, Egridir and Antalya, all specimens, of which I could examine the genitalia, are *ponticus* without any trace of *malvae*.

The fact that transitional specimens between *malvae* and *ponticus* are unknown does not mean that these do not occur, as the western part of Turkey has not been carefully investigated. As compared with the situation *malvae* - *malvoides*, we can only state that *ponticus* and *malvae* potentially interbreed and therefore I place *melotis* (with the subspecies *melotis* and *ponticus*) as a semispecies in the superspecies *malvae*.

The *alveus* complex

Male genitalia. — Lateral apophyses not connected by a lamina transversa, only connected by a membrane. The ventral part of the lateral apophyses is strongly sclerotized, more or less triangular and with a convex, straight or concave, strongly spined dorso-distal edge. Uncus slender, with a hooked apex (that may be split longitudinally). Cuiller well-developed, at least about a semi-circle (*P. armoricanus*). Valvae, Fig. 36—45.

Female genitalia. — Without a distinct genital plate, at most two sclerotized, post-vaginal spots.

Facies. — Variable. Median spot 5 unh usually without a projection towards the base of the wing.

There is much confusion in literature about the taxonomy of this species complex. The following forms have been given specific rank on a certain day (arranged alphabetically): *accretus*, *alveus*, *armoricanus*, *bellieri*, *cinarae*, *iliensis*, *jupei*, *kansuensis*, *numidus*, *reverdini*, *scandinavicus*, *schansiensis*, *sifanicus*, *speyeri*, and *warrenensis*. It seems desirable to review all these forms critically in order to arrive at an acceptable taxonomic division.

No problems have been caused by the forms *armoricanus*, *bellieri*, and *cinarae*. They have always been regarded as separate species, at least since the work of Reverdin at the beginning of this century.

P. cinarae deviates from the other types with regard to the male genitalia by a very long uncus, and a broad, flat style which is folded over, a character only found in a number of species of the subgenus *Scelotrix*. Also stylifer and antistyle are broad. The female genitalia are characterized by the undeveloped postvaginal region.

The regular, semicircular type of cuiller found in *P. armoricanus* cannot be mistaken. The ventral part of the lateral apophyses has a convex dorso-distal edge, distinct from the usually concave edge in the other forms of the subgenus. The female genitalia lack a distinct antevaginal plate which is present in the other forms. Very rarely *P. armoricanus* and *P. alveus* fly together. This may be the case in the southern Alps where Kauffmann & de Bros (1952) found a few specimens of *P. armoricanus* with some features of *P. alveus* in the shape of the cuiller and of the lateral apophyses. It is not certain whether these are hybrids, but if so, they must be the results of very incidental cases of hybridization that still demonstrate the close relationship between *P. armoricanus* and *P. alveus* but that do not devalue the specific rank of *P. armoricanus*.

In *P. bellieri* we find the most developed type of cuiller, amply reaching more than half of the total length of the valve, with a large ventro-distal bulge.

The ventral part of the lateral apophyses is short, with a more or less concave dorso-distal edge. In the female genitalia there are three postvaginal lobes, instead of two, as in the other forms (except in *P. cinarae* which lacks postvaginal lobes).

There is only one form which closely approaches *P. bellieri*, viz. *accretus*. They come into contact in the SW Alps, both at the French and the Italian side. Occasionally specimens have been found with transitional characters. Warren sent me a photograph of such a specimen from Cesane (Piedmont) and I saw two specimens from the Basses Alpes. This suggests that (very rarely) hybridization occurs.

The taxonomic position of *warrenensis* is still rather uncertain, but I am inclined to assign to it specific rank and, I shall deal with it below, as a species. In the original description by Verity it was thought to be an extreme variation of *P. alveus*, confined to the high altitudes of the Alps. Warren (1953), however, showed that it is quite distinct from *P. alveus*, externally as well as in the male genitalia and that it may fly with *P. alveus*, evidently without producing transitional forms. He even states that in the localities in which *warrenensis* and *alveus* occur together the former emerges at least ten days before *alveus*, and is quite worn when the latter is fresh. Some specimens from the Gross Glockner region, however, are difficult to identify and I think hybridization occasionally occurs there. Besides, if we consider the matter from other side, the statement of Warren that *warrenensis* emerges earlier than *alveus*, doesn't settle the

matter: *warrenensis* is adapted to a high altitude environment and therefore emerges as early as *alveus* in spite of this higher altitude; in the course of the flight period the weather becomes warmer and *alveus* ascends into the regions of *warrenensis*, but only individuals of *alveus* that have emerged late in the season may reach the *warrenensis* habitat. Of course, there is no proof of this, but it shows that the position of *warrenensis* is still uncertain and that the interrelation between *warrenensis* and *alveus* can only be made clear by a study on the spot.

Warren (l.c.) placed *warrenensis* as a subspecies in the species *sifanicus* (see below), an incomprehensible action, if one does not take into account the fact that Warren misjudged the position of the latter form.

The form *sifanicus* has been surrounded by confusion since Reverdin (1915) identified *alveus*-like specimens from the Caucasus and Transcaucasia as *sifanicus* which originally was described from the Kuku-Nor region (N Tibet) by Groum-Grshimailo (1891). Only in 1967 Alberti explained the situation in the Caucasus and Transcaucasia by showing the occurrence of three forms in that region: one form like the N Tibetan *sifanicus*, another form indistinguishable from the C European *alveus* and a third, that he named *jupei*. Warren (1968, in litt.) is of the opinion that *jupei* is only an extreme variation of a variable *sifanicus*. It is interesting to note that the photograph of the male genital armature of "*sifanicus*" from Borshom in Reverdin (1915, pl. 6 fig. 6) and evidently of the same microscopical slide, in Warren (1926, pl. 9 fig. 6) shows the typical structure of *jupei*, while, as far as I know, the male genital armature of *sifanicus*-like specimens from Transcaucasia has been figured by Alberti only (1967, pl. 1, figs. 1-c, 2a-c). However, the *warrenensis* type of genitalia resembles the *jupei* type and not the *sifanicus* type, especially with respect to the raised apex of the cuiller (compare Fig. 44 and 45). Furthermore, *jupei* is characterized by the very small style-stylifer-antistyle, the height of antistyle + stylifer being about half of the total depth from the base of the style to the ventral edge of the valve. Also in *warrenensis* it may be rather small, but it is larger than in *jupei* and the style is longer.

Externally *jupei* and *warrenensis* are quite distinct *jupei* being a larger and usually better marked form. Although the similarity between *jupei* and *warrenensis* may be due to a common ancestor, I do not see any reason to unite them into a single species, as Warren did with *warrenensis* and *sifanicus*. Whereas *warrenensis* is confined to the high altitudes of the Alps, *jupei* only occurs in the high altitudes of the Caucasus region. Specimens transitional to *alveus* are not known, but, as a matter of fact, the Caucasus region is much less explored than the Alps. Like *warrenensis*, *jupei* will be treated here as a separate species.

There is another form that has been regarded by Warren (1953) as conspecific with *sifanicus*, viz. *numidus*. This form represents the *alveus* complex in NW Africa where it flies in the mountains from 1700 to 2700 m. Indeed, the male genitalia of *numidus* with the highly raised apex of the cuiller, are very suggestive of *warrenensis*. In size and design *numidus* and *warrenensis* represent about the extremes of variation in the *alveus* complex, *numidus* being one of the largest and most extensively spotted forms, *warrenensis* the smallest and least spotted form. Of all forms of the *alveus* complex *numidus* can be distinguished by the anvil-shaped central spot, unh, being in this respect very similar to the large N African *Pyrgus onopordi*.

As in the case of *jupei* I do not see any reason for considering *warrenensis* and *numidus* conspecific. Moreover, a form occurs in the Sierra Nevada, externally similar

to *numidus* but with the male genitalia intermediate between *numidus* and *centralhispaniae* (belonging to the form *accretus*): it possesses the narrow cuiller of *numidus*, but apically the cuiller bends over to the harpe as in *centralhispaniae*. Possibly this form represents a hybrid population of *accretus* and *numidus*. Therefore, I regard *numidus* and *centralhispaniae* (and for that matter *accretus*) conspecific.

The form *accretus* is characterized by the short free proximal edge of the cuiller which slopes towards the harpe and even may nearly touch it. Besides that, the cuiller has a ventro-distal expansion, not as marked, as in *bellieri*, but usually obvious. Another character of *accretus* is the short ventral part of the lateral apophyses and the long shaft that connects it with the dorsal part. With some geographic variation this form is distributed throughout Spain and France and penetrates a little into NW Italy. According to Warren (1953) it has been found together with *alveus* and *bellieri* near St. Martin Vésubie (Alpes Maritimes), together with *bellieri* at Limone (Piedmont, Ligurian Alps) and probably together with *alveus* at Oulx (Piedmont, Cottian Alps). He also supposes a sympatric occurrence with *alveus* in the Swiss Jura. However, his figures of an *alveus* type specimen and an *accretus* specimen (Pl. 7, Fig. 3 and 4) taken flying together at St. Martin Vésubie do not indicate any more than that both types occur at the same spot. It does not prove that *alveus* and *accretus* are unable to interbreed. Indeed, examining the genitalia of eight males from St. Martin Vésubie, I found four specimens of the *alveus* and two specimens of the *accretus* type of genitalia and two specimens with intermediate characters. I also saw some transitional specimens from Haute Savoie. It is interesting to note that Kauffmann (1953) recorded the occurrence of *accretus* in SW Germany where also *alveus* flies, but where it is found later in the season. Evidently, *alveus* and *accretus* interbreed and although the interbreeding doesn't seem to have led to extensive hybrid populations, I prefer to regard *accretus* only subspecifically distinct from *alveus* until a detailed study of both forms in the western and southern Alps has revealed their interrelations.

As *accretus* can be subdivided into geographic forms I will distinguish a subspecies group *accretus* (see further below, Chapter 3). Of course, this decision is as subjective, as that of Warren (1953), who raised *accretus* to specific rank. Evans (1956) says (p. 749): "I have failed to separate *accretus* as a subspecies from *alveus*", an incomprehensible observation, as they are easily separable.

The form *alveus* is characterized by: (1) the free proximal edge of the cuiller is about vertical to the ventral line of the valve, its length being about one third the total depth of the proximal edge of the cuiller (in *accretus* less than one third); (2) the apex of the cuiller is level with the dorsal ridge of the harpe or slightly above it (unlike *warrenensis*, *jupei* and *numidus*); (3) the outline of the cuiller is nearly circular or partly flattened, without a ventro-distal bulge; (4) the ventral part of the lateral apophyses is larger than in *accretus* and consequently the shaft is shorter. With considerable individual and slight geographic variation this form extends from Central Europe to the Altai. Even some specimens from the Kuku-Nor region cannot be distinguished from C European ones. The only real difference with *sifanicus* is the white border of the underside of the wings in the latter, while in *alveus* such white borders are very rare, particularly unh. Evans (1949) regarded all specimens from the Caucasus to Kuku-Nor as *sifanicus* but this is obviously wrong as the white borders of the wings, below, only occur in specimens from the Kuku-Nor region and from Transcaucasia (and N Iran). From the Kuku-Nor region I examined nine males and one

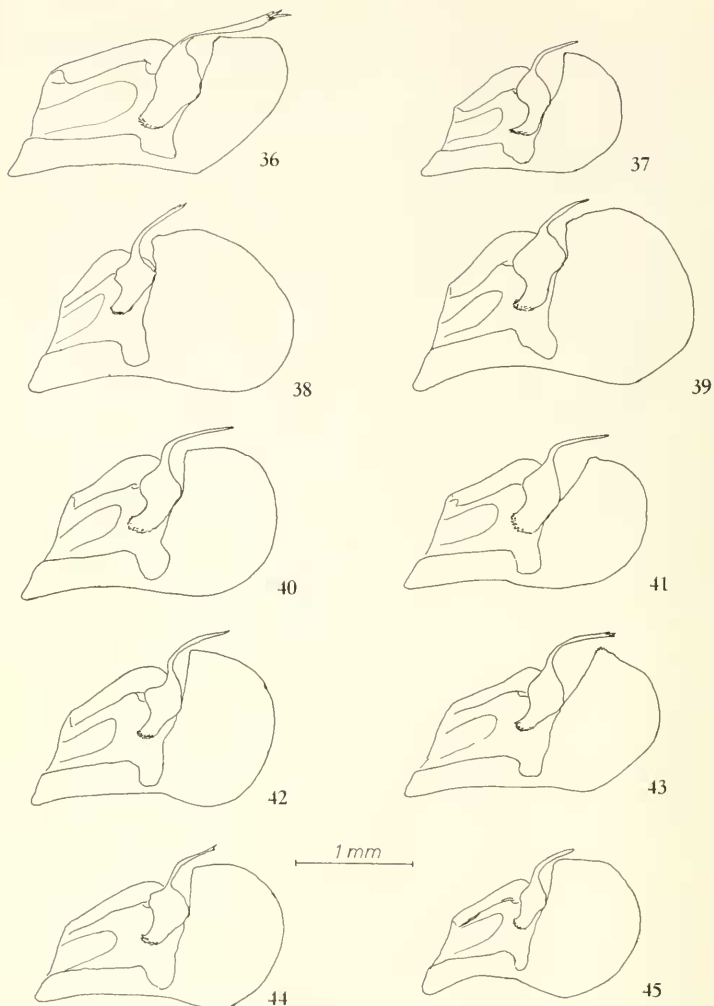


Fig. 36—45. Male genitalia (right valve). 36, *Pyrgus cinarae* (S Russia); 37, *P. armoricanus* (C Italy); 38, *P. bellieri* (Digne, SE France); 39, *P. alveus accretus* (C Pyrenees); 40, *P. alveus alveus* (Swiss Alps); 41, *P. alveus scandinavicus* (Beito, Norway); 42, *P. alveus numidus* (Morocco); 43, *P. alveus speyeri* (Kentei); 44, *P. warrenensis* (Gross Glockner); 45, *P. jupei* (Kasbegi, C Caucasus)

female; only five males and the female showed obvious white borders, the other males more closely resembled the C European *alveus*. In the Caucasus region the *sifanicus* type seems to be mainly confined to Transcaucasia and even there many specimens can hardly or not at all be separated from the C European *alveus*. The male genitalia do not warrant a specific separation of *sifanicus* either, as was done by Warren (1953) (see above, under *warrenensis* and *jupei*). I examined the genitalia of four males from Kuku-Nor and four (more or less *sifanicus*-like) males from Transcaucasia. They show some variation (one male from Transcaucasia has a highly raised apex of the cuiller but is otherwise quite different from *jupei*) but the variation seems to fall within the variation width of *alveus*.

Kauffmann (1954a) dealt with the variation (particularly in the male genital armature) of *alveus* in the southern Alps (Insubria); in a confused and confusing manner he named these populations *iliensis columnus*, thus considering them conspecific with the form *iliensis*, described from the river Ili (N Turkestan). Undoubtedly this conspecificity is right, but the specificity of *iliensis* is without any foundation; I can only regard it as a subspecies of *alveus*. According to Warren (1953) *iliensis* belongs to the *speyeri* group (see below) but I do not understand how he arrived at this conclusion.

In Scandinavia the *alveus* complex is represented by a form (*scandinavicus*) characterized by the distad slant of the proximal edge of the cuiller, which often gives the impression that the cuiller is bent backwards; the length of the free part of the proximal edge of the cuiller is slightly more than in *alveus*; the cuiller is dorsally usually more developed than ventrally and the antistyle is usually broader than in *alveus*. Warren (1953), examining 28 males from Scandinavia, found a single specimen from Gjendestunga (Jotunheim), with genitalia of the *alveus* type. As also the *scandinavicus* type was known to occur there, he promoted *scandinavicus* to the specific rank. Opheim (1956), however, examined the male genitalia of about one hundred specimens from Norway and a single one from Gotland and observed a fairly continuous variation from the *scandinavicus* type to the *alveus* type; consequently, he assigned to *scandinavicus* subspecific rank only. I could examine the male genitalia of about 40 specimens from Scandinavia and can support Opheim's view.

It is interesting to note that the formation of the cuiller found in *scandinavicus* resembles in some specimens the formation in the Chinese form *reverdini*. This has led to very confusing remarks by Warren on the specificity of *reverdini*. Without knowing the *scandinavicus* type of genitalia, Warren (1952) dissected a male from Sylkynjärvi (Finland) and found the genitalia similar to a photograph by Reverdin (the same as Warren, 1926, Pl. 6, Fig. 2) of *reverdini* and as the specimen had been taken flying with a "perfectly typical" male of *alveus* (of which Warren did not dissect the genitalia), he concluded that *reverdini* was specifically distinct from *alveus*. Besides, he compared the habitus of the Finnish "*reverdini*" with the figures 1216 and 1217 of Oberthür (1912) (belonging to the original description) and as the Finnish specimen was somewhat different, he erected for it a new subspecies *scotti*!

In 1953 he had still not seen more of the Chinese *reverdini* than the photograph mentioned in his 1952 paper. But he had studied the genitalia of *scandinavicus* and of the "perfectly typical" male of *alveus* which had been taken flying with *scotti*, and which turned out to have the genitalia of the *scandinavicus* type (i.e., according to Warren, the *reverdini* type). The subsequent taxonomic change was drastic, *scandinavicus* be-

coming a species, *reverdini* a subspecies of *scandinavicus* and *scotti* a form of the nominate subspecies (sic!).

Apart from the fact that such actions do not promote real systematics, the nature of *reverdini* remained entirely obscure. Kauffmann (1952) even doubted its subspecific value, though he never saw a specimen of it.

I have examined the male genitalia of four specimens of *reverdini* (apart from the photograph in Warren, 1926). They show some variation and are as much suggestive of *alveus* as of *scandinavicus*. This also means that they are difficult to distinguish from the structure, found in *sifanicus* of the Kuku-Nor region. In addition *reverdini* and *sifanicus* share the white borders at the underside of the wings. There is, therefore, no reason to give *reverdini* more than subspecific rank.

There are still three forms left to deal with, all three Asiatic ones. One of these, *kansuensis*, described by Reverdin, is entirely obscure and I doubt whether anybody except Reverdin ever saw this form. Its locality suggests a close relationship, if not identity with *sifanicus*, but it is better to leave *kansuensis* here out of consideration.

Another rare but somewhat better known form is *schantziensis*. Though only very few specimens have been described, it seems to be rather constant over a large area from Shan Si to north of the river Amur. With regard to external characters, it resembles *alveus*, although it is much larger. As to the male genitalia, it differs from *alveus* by the very long ventral, spined part of the lateral apophyses, a character I also found developed to some extent in a number of *speyeri* specimens. The cuiller appears to be better developed dorsally than ventrally. Apart from the fact that the ranges of *schantziensis* and *speyeri* seem to overlap to a certain extent, there is no reason to place *schantziensis* otherwise than as a subspecies of *alveus*. The fact that *schantziensis* and *speyeri* are very different, leads us to the assumption that both forms do not interbreed; while considering *schantziensis* and *alveus* conspecific it is sensible to consider *speyeri* specifically distinct.

The form *speyeri* may be the best known Asiatic form of the *alveus* species complex. It is widely distributed in Transbaicalia and the Amur district. I examined the genitalia of fifteen males and found very much variation. The proximal edge of the cuiller is vertical to the ventral line of the valvae, as in *alveus*, or slopes backwards, as in *scandinavicus*. The antistyle is broad and straight, as in *scandinavicus*, or slender and hooked, as in *alveus*. The apex of the cuiller, usually very solid and spined, is level with the dorsal edge of the harpe in some specimens, but in most it is raised high above that edge. Usually the cuiller is dorsally better developed than ventrally, having a somewhat *scandinavicus*-like appearance. The free proximal edge of the cuiller is more than one third the total depth of the cuiller, as in *scandinavicus*, and in some specimens even reaches half of the total depth of the cuiller. The ventral part of the lateral apophyses is also variable, sometimes suggestive of the *schantziensis* type but usually shorter. Externally *speyeri* is an unmistakable form, though there exists some variation (see Chapter 3). However, west of the Lake Baikal matters become complicated. There it seems impossible to make a sharp distinction between *speyeri* and *alveus* (and *scandinavicus*!). Details will be given in Chapter 3. It makes me doubt the specific rank of *speyeri* and, though it is not a very satisfactory solution, I am placing *speyeri* as a subspecies of *alveus*, and *schantziensis* as a separate species. However, only abundant material and research on the spot can clarify the relations between the Asiatic forms of the *alveus* complex.

Summarizing, in this study the following species have been recognized within the *alveus* complex: *alveus*, *armoricanus*, *bellieri*, *cinarae*, *jupei*, *schansiensis* and *warrenensis*. Other forms, by some authors considered specifically distinct, have been placed here as subspecies of *alveus*. In this review I have only given the general outline of the variation. Many details may be found (at least of the European forms) in Warren (1953) and Kauffmann (1954). I must, however, stress the fact that much of the confusion about the *alveus* complex is due to a too detailed examination of a too limited material which has led to attaching too much value to details. Of course, the present classification cannot be regarded as definitive, and only is an attempt to summarize the relations within the entire *alveus* complex.

Species of uncertain affinities

In some respects, the species classified here seem intermediate between the subgenus *Scelotrix* and the *alveus* species complex. The females possess a genital plate, but it is entirely embedded in the membrane and not free, as in *Scelotrix*. The male genitalia (Fig. 46-49) resemble the type found in the *alveus* species complex by the sharp, hooked apex of the uncus and by the absence of a ventral connection between the lateral apophyses. The valvae are as much *Scelotrix*-like as *alveus*-like. The lateral apophyses are very characteristic. In *P. serratulae* the ventral part of the lateral apophyses is very large and strongly spined; although not connected ventrally, the ventral parts are yet solidly connected by a strongly curved, sclerotized, smooth

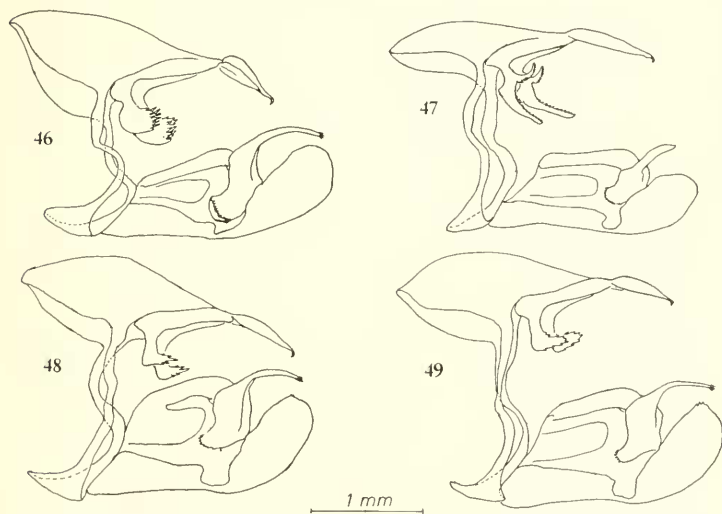


Fig. 46—49. Male genitalia. 46, *Pyrgus serratulae* (S France); 47, *P. onopordi* (S France); 48, *P. carlinae* (Val d'Aosta); 49, *P. cirsii* (C Spain)

bridge, with a very concave ventral surface and embedded in the anal sheath. In *P. onopordi* the ventral part of the lateral apophyses is bipartite, with a long ventral and a short dorsal projection, both spined. In the superspecies *carlinae* the ventral parts of the lateral apophyses are rather simply built, somewhat elongated and strongly indented. They recall to a certain degree the type found in *malvoides* (subgenus *Pyrgus*), but are better developed and lack the lamina transversa of that semispecies.

Other separating characters can be found in the aedeagus which is strikingly broad in *P. onopordi* and spined in the superspecies *carlinae*, a unique feature in the Palaearctic species of *Pyrgus*.

As these species appear to be closer to *Scelotrix* than to the *alveus* species complex, they will be dealt with in Chapter 3 before the *alveus* species complex.

The American *Pyrgus* species

Apart from *centaureae* which undoubtedly is a rather recent invader from Asia (see Chapters 2d and 3) the American *Pyrgus* species are quite different from their Palaearctic congeners. From a phylogenetic point of view, however, the following notes are of importance.

(1). All American species have a white spot at the base of space 2 upf, as in a number of species of the subgenus *Scelotrix*.

(2). Though variable the males of the American species have a lamina transversa or something resembling it. In *P. oilens* I even found a lamina transversa which is difficult to distinguish from the type found in subgenus *Scelotrix* and in a form of *P. communis* (*orcynoides*) the (unspined) lamina transversa appeared to be ventrally concave, thus suggesting the "bridge" of *P. serratulae*.

(3). In the American species the uncus is bipartite, but unlike *P. malvae* the two parts are situated close together (more suggesting *malvae kauffmanni*, see Chapter 3).

In conclusion, the American species appear distantly related to the subgenus *Scelotrix*, while their relationship to the *alveus* species complex is only evident through the subgenera *Pyrgus* and *Scelotrix*.

2.c. Distribution

The distribution of the genus *Pyrgus* in the Palaearctic is very extensive, it comprises the entire Palaearctic, with the exception of desert regions. The distribution in N and NE Siberia is unknown.

Of the eleven species of the subgenus *Scelotrix* (including one superspecies) six are confined to Asia, one is Holarctic, two are cold-adapted European species and two have a mainly European distribution.

The subgenus *Pyrgus* has a Palaearctic distribution.

The remaining ten species (including one superspecies) in the Palaearctic are mainly European, only *P. serratulae* and the *alveus* complex extending far into Asia, thus giving a distribution opposite to that of the subgenus *Scelotrix*.

In America the genus is distributed from Canada to Chile and Patagonia. Of the twelve species recognized by Evans (1953) six species are confined to S America. There is still little agreement about the classification of the American *Pyrgus* species, but a different classification can only increase the number of S American species. Apart from *P. centaureae* only two species (in the classification of Evans), *P. ruralis* and *P. communis*, extend to north of the Sonoran region.

2.d. Geographic and evolutionary history

The geographic origin of the genus is very uncertain. It would fall too far outside the scope of this work, to elaborate on the systematics of the S American species, but they are undoubtedly descendants of N American invaders. A Neotropic origin of the genus can therefore be left out of consideration. The following statements can be made.

(1). The genus is of Holarctic origin.

(2). The contact between the Palaearctic and Nearctic groups was severed very long ago, at some time during the Tertiary. The recent distribution of the species suggests an originally thermophilous group. Whether the contact was re-established later is difficult to say, but during the Quaternary contact was only possible through cold-adapted species. Indeed, *centaureae* migrated into America in rather recent times (see also below).

(3). Apparently, in the Palaearctic, the subgenus *Scelotrix* has the most primitive characters as it has some characters in common with the American species, which among all others are the only ones to be considered primitive.

(4). There are no indications of an invasion from the Nearctic into the Palaearctic.

(5). The bipartite uncus of *malvae* appears to be a young character and is not an indication of a close relationship to the American species. All other characters, of the male as well as of the female genitalia of *malvae*, indicate a recent origin, compared to *malvoides* with which *malvae* still hybridizes to some extent.

In the Palaearctic members of the genus, the uniformity in the male and female genitalia of the subgenus *Scelotrix* is striking, at least, in comparison with the other species of the genus. This uniformity concerns the genital plate of the female and the dorsal parts (uncus and lateral apophyses) of the male genitalia. The meaning of this (relative) uniformity is not yet known, but apparently it is not because *Scelotrix* has remained unchanged from the time that the contact with the Nearctic disappeared (see also the history of *Scelotrix*, below). Apparently, the breakdown of the *Scelotrix* structure of genitalia has accelerated the evolution, subsequently giving rise to many divergent types. This occurred presumably more than once. Therefore I cannot unite e.g. *P. serratulae* and *P. alveus* into one subgenus and fail to see, why *P. carlinae* would be more closely related to, e.g. *P. alveus* than to *P. malvoides*.

The principal development of the genital plate and the lamina transversa of the lateral apophyses appears to have been a reduction and subsequent disappearance.

Special attention may be drawn to the supposed evolution of the lateral apophyses. In *Scelotrix* they form a complete ring around the anal sheath, to which they are more or less attached. The lamina transversa supports the anal sheath ventrally and e.g. in *P. maculatus* it has a long sclerotized projection towards the distal end of the anal sheath. Presumably, the spined lamina transversa serves as an extra grip during copulation. Where it is reduced its supposed function is taken over by spines springing from the ventral part of the lateral apophyses. I have tried to illustrate a possible course of the evolution in Fig. 50. It is impossible to believe that the *malvoides* and the *serratulae* types belong to the same evolutionary trend. The other types (*carlinae*, *onopordi*, *alveus*), if not evolved directly from a *Scelotrix* type, may have originated equally well from the *serratulae* type as from the *malvoides* type.

In addition an attempt is made to reconstruct the outline of the tentative geographic

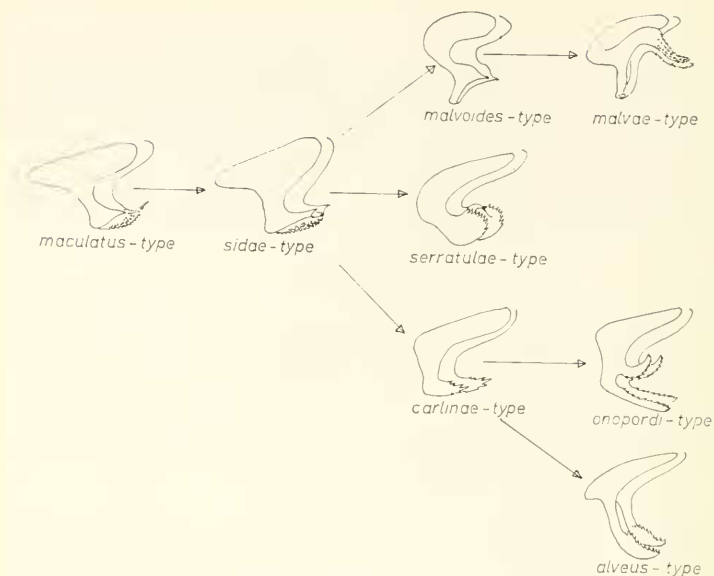


Fig. 50. Possible evolution of lateral apophyses in *Pyrgus*

history of the genus in the Palaearctic. The distribution, variation and relationship in Asia of *P. malvae*, *P. serratulae* and the *alveus* complex strongly suggest that they are newcomers in that continent and invaders from Europe. On the other hand, the same can be said of the *centaureae* group (*centaureae*, *cacaliae*, *andromedae*) of *Scelotrix* in Europe, while the other *Scelotrix* species in Europe (*carthami*, *sidae*) appear taxonomically more distant from Asiatic species.

Thus, the geographic history of the genus may be outlined as follows. At some time during the Tertiary period *Scelotrix* extended throughout the Palaearctic. The geographic origin of *Scelotrix* cannot be defined more exactly. Somehow, the European part of the genus became isolated and has developed characters of its own. This separation of the European group was followed by a new invasion of *Scelotrix* into Europe, a subsequent isolation, etc. This occurred several, if not many times, giving rise to the *serratulae* and *malvoides* types of genitalia, respectively. *P. carthami* and *P. sidae* may have originated in the same way. The last invasion of *Scelotrix* brought *centaureae* to Europe (see below, the history of the subgenus *Scelotrix*).

It is impossible to date the successive invasions more or less exactly, apart from the more recent invasions of the *centaureae* group. Therefore, the causes of isolation of the European groups remain uncertain. The following considerations, however, may be of interest.

(1). As stated above, the genus was thermophilous (at least adapted to a temperate

climate), when the contact with the Nearctic has been severed. Such a group had ample possibilities of being distributed throughout the Palaearctic in Tertiary times (cf. Petersen, 1954; Moreau, 1955).

(2). Though the subgenus *Scelotrix* may be supposed to have the most primitive characters of the genus in the Palaearctic, only three species (*P. maculatus*, *P. carthami* and *P. sidae*) appear to be adapted to a temperate climate, while the other species are cold-adapted (see also the history of the subgenus *Scelotrix*, below).

(3). None of the cold-adapted *Pyrgus* species outside the subgenus *Scelotrix* can be regarded as a direct descendant of a cold-adapted *Scelotrix* species (see also below).

(4). From this follows that the adaptation to a cold habitat in *Scelotrix* and in the rest of the genus is secondary. Consequently the adaptation to high altitudes of Asiatic *Scelotrix* species may have contributed to the isolations of the European groups. The gradual rise of the Asiatic mountains may have forced this adaptation (see below).

(5). Of course, also the cooling down of the Palaearctic in Pleistocene times may have influenced the contact between the European and Asiatic members of the genus, but apart from the *centaureae* group this influence is obscure.

Summarizing the geographic history of the genus, we may state that the subgenus *Scelotrix* has a Palaearctic origin, while all other Palaearctic species have a European origin (or originate from a European species).

Asiatic species invaded Europe many times, giving rise to several new species by subsequent geographic isolation. Some European species re-invaded Asia and in the *alveus* complex this may have given rise to species duplication in Asia (see below). The geographic history of *Scelotrix* and of the *alveus* species complex will be outlined below; that of the other species will be dealt with in Chapter 3 (including the geographic history of the species of *Scelotrix* and the *alveus* species complex).

Geographic history of the subgenus *Scelotrix*

The general uplift of the Asiatic mountains lasted until rather recent times. According to Kostrowicki (1969) the Kunlun was even elevated during the Pleistocene by 1300-1500 m above its level of the first glaciation. This must have been of great influence on the geographic history of the species of the subgenus as it may have forced some species to adapt themselves to a much colder habitat. But apart from such a general statement it is difficult to indicate the influence more exactly. This is partly due to the lack of knowledge on the present distribution in Tibet. From the scanty data available one may assume that e.g. *P. oberthuri* and *P. dejeani* are widely distributed throughout Tibet, but as long as they are only known from border areas one cannot be sure. Nevertheless, their known distribution (E Tibet, Turkestan/Transcaspia) suggests that they belong to the fauna that has been forced to submit to an adaptation to rough climatic conditions during the time of the uplift of the Tibetan highlands.

It is clear that the cold-adapted Asiatic species must be regarded as having originated in Asia, while the warmth-loving *P. carthami* (European distribution) and *P. sidae* (mainly Mediterranean distribution) may be regarded as remnants of the old, warmth-loving *Scelotrix* group. Although its ancestors may have been Asiatic, *P. carthami* undoubtedly became separated from related forms in Europe. The geographic origin of *P. sidae* may have been the western, warmer part of Central Asia and also the Mediter-

ranean. The E Asiatic *P. maculatus* (the only *Pyrgus* species that has reached Japan) may also be regarded as a remnant of (or a descendant from) the thermophilous *Scelotrix* group. Like *P. sidae* it has developed a particular unh. Its origin, however, is obscured by the presence of a subspecies in the mountains of Szechwan and by the presence of a probably closely related species, *P. bieti*, in the mountains of Szechwan and Yunnan.

Turning again to the cold-adapted species, the history of *P. badachschanus* isolated by its structural features and restricted to N Afghanistan is entirely obscure. The presence of a white spot at the base of space 2 upf may indicate its high antiquity. The super-species *alpinus* is known from the same region, but has a much wider distribution, extending from Kashmir and Afghanistan through Pamir to N Turkestan and the Altai as far as Kamschatka. As will be seen in Chapter 3, the distribution north and east of Turkestan is supposed to be of recent age and the origin of the superspecies has to be looked for in Pamir and adjacent regions.

According to Warren (1926), *alpinus* is closely related to the *centaureae* group (*P. centaureae*, *P. cacaliae* and *P. andromedae*), but I am not able to understand, why their relationship to the *centaureae* group would be closer than to other *Scelotrix* species.

The geographic history of the *centaureae* group may be outlined as a repeated expansion to Europe. Of the three species *P. andromedae* appears to be the least modern. This is not only indicated by the presence of a white spot at the base of space 2 upf (rarely present in *P. centaureae*, too), but also indirectly by the fact that some specimens of *centaureae sibiricus* resemble *P. cacaliae* in the washed-out appearance of the wings. Presumably three waves of migration from Siberia to Europe occurred, successively bringing *P. andromedae*, *P. cacaliae* and *P. centaureae* to Europe.

In Chapter 3 the last invasion into Europe is supposed to be of postglacial date. Thus the invasion from which the present *P. cacaliae* originated may be tentatively dated at the Third Glacial, while the first invasion (*P. andromedae*) may have taken place during, or shortly after, the Second Glacial. However, in Chapter 3 the expansion of *P. centaureae* into America has been dated at the Third Glacial, i.e., the same glacial during which *P. cacaliae* is supposed to have reached Europe. Externally, in the male and in the female genitalia the Nearctic and the Palaearctic *centaureae* forms are closer to each other than to *P. cacaliae*, suggesting that the contact between the Palaearctic and Nearctic *centaureae* forms has been severed later than the contact between Siberian *P. centaureae* (as far as we can speak of *centaureae* in that period) and European *P. cacaliae*. This is quite possible, as *P. cacaliae* may have reached Europe at the beginning of the Third Glacial and may soon have lost contact with Siberia.

According to the above reconstruction of the geographic history, *P. cacaliae* and *P. andromedae* appear to be species that in Europe became specifically distinct from the Siberian populations from which they originated, while *centaureae* received its specific imprint in Siberia from where it spread to Europe and America.

At present the Scandinavian form of *P. centaureae* (ssp. *centaureae*) is distinct from the Siberian form (ssp. *sibiricus*). In the male genitalia the ssp. *centaureae* appears to differ less from the American forms than from ssp. *sibiricus* (the female genitalia have been left out of consideration, because of their great variability). In some specimens of ssp. *sibiricus* the cuiller is quite narrow and elongated which seems to be a recent character. Thus it appears that if ssp. *centaureae* and ssp. *sibiricus* will eventually become specifically distinct, it will be due to a differentiation of ssp. *sibiricus* and not

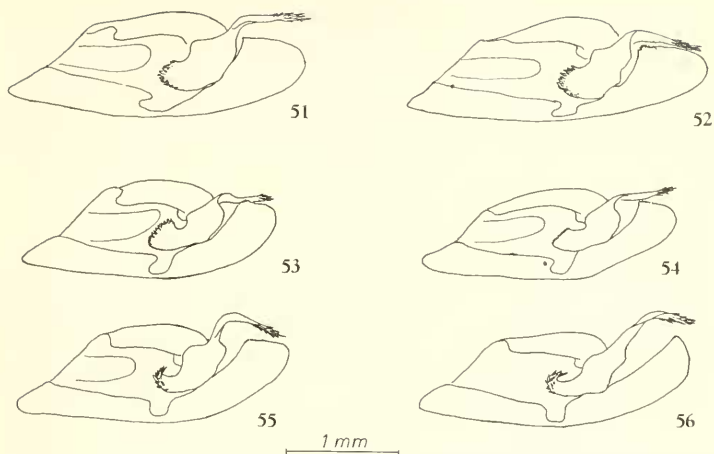


Fig. 51—56. Male genitalia (right valve). 51, *Pyrgus andromedae* (Abisko, Sweden); 52, *P. cacaliae* (Tirol); 53, *P. centaureae centaureae* (Lapland); 54, *P. centaureae wyandot* (New York); 55, *P. centaureae sibiricus* (Altai); 56, *P. centaureae sibiricus* (E Sajan)

of ssp. *centaureae*. Thus both will still have to be called Siberian species, as both originated there.

Virtually the male genitalia of the *centaureae* group are suggestive of such a development. The general evolutionary trend of the valve appears to be a widening of the gap between the distal edge of the harpe and the proximal edge of the cuiller, followed by a narrowing of the cuiller. Thus, in *P. andromedae* the free proximal edge of the cuiller practically touches the terminal curve of the harpe. In *P. cacaliae* the edge of the cuiller is very close to the harpe but does nowhere touch it, while in *centaureae centaureae* the harpe and the free proximal edge of the cuiller are clearly apart and in some specimens of *centaureae sibiricus* they are far apart (Fig. 51—56). Apparently, a repeated differentiation in the *centaureae* group took place in Siberia and not in Europe. The denomination of *P. cacaliae* and *P. andromedae* as European species is therefore, at least, debatable. Indeed, the far-reaching intergradation of the Siberian and European faunas is much more apparent in the denomination of *P. cacaliae* and *P. andromedae* as Siberian species than as European species.

The fact that *P. cacaliae* and *P. andromedae* at present have retained some original characters does not mean that they are identical to their parental Siberian populations. Undoubtedly a part of the present characters evolved in Europe, but this does not alter the fact that they were Siberian when they became specifically distinct from other forms.

If the Siberian populations had evolved at a slower speed and had retained more of the original characters than the European ones, *P. cacaliae* and *P. andromedae* would have been regarded as European species as they (apparently) would have received their specific imprint in Europe.

Phylogenetically the difference between a European and a Siberian origin in the cold-adapted species appears gradual and not essential. The conception may be tenable that a species ceases to exist when it is split into two or more intersterile forms, but of course this is only a matter of definition (see also Chapter 4.a).

Unlike *P. centaureae*, *P. cacaliae* and *P. andromedae* do not belong to what is usually meant by the denomination "Siberian fauna", i.e. the fauna of the taiga (coniferous) zone. They belong to the fauna of the alpine meadows. For their zoogeographic classification, see Chapter 5.

The geographic history of the *alveus* species complex

As stated above the origin of the *alveus* species complex is obscure, but it may be called a European group of species. In Asia (apart from the eastern Mediterranean) it is only represented by *alveus* and *schantziensis*. This is a poor representation as compared with the six species in Europe, the more so as the specific rank of *schantziensis* is debatable (it could be a subspecies of *P. alveus*). The slight differentiation in Asia, the absence south of the Issyk-Kul (except *P. cinarae*?) and the fact that the least modern species of the complex, *P. cinarae* and *P. armoricanus*, are European, lead to the assumption that the *alveus* species complex has a European origin and that it invaded Asia from Europe.

The supposition, that *P. cinarae* and *P. armoricanus* are the least modern species of the complex, is based on the fact that they stand taxonomically somewhat apart, while all other species are extremely close to *alveus*; also because of their preference for a warm climate, while the other species prefer a more temperate or even cold climate. The geographic origin of *P. cinarae* and *P. armoricanus* cannot be defined more exactly than it is European, but ecologically they do not belong to the same fauna, see Chapters 3 and 5.

The history of the other species can be reconstructed with a fair degree of probability.

The present distribution area of *P. bellieri* (SE France, NW Italy, C Italy) strongly suggests an origin in an Italian refugium during some glaciation. In external characters and in the male genitalia *P. bellieri* is an extreme variation of the SW European *accretus* group (subspecies group of *P. alveus*) and undoubtedly they share a common origin. As the occurrence of *P. alveus* in C Italy (ssp. *centralitaliae*) probably dates from the Last Glacial (see Chapter 3), the origin of *P. bellieri* and the *accretus* group cannot have been later than the Third Glacial and there is no reason to assume an earlier origin. The origin of *P. warrenensis* (Alps), *P. jupei* (Caucasus) and *alveus numidus* (N Africa) must have been earlier and may be dated at the Second Glacial. The fact that they share some characters of the male genitalia (mainly the raised apex of the cuiller, but also the more or less even width of the harpe) may be due to their common origin. Though the resemblance appears rather slight and of little importance in view of the variation in the *alveus* complex, one cannot expect to find a total resemblance between forms that have been isolated from each other since the Second Glacial. I think it even possible that the E Asiatic *alveus speyeri* belongs to this Second Glacial group. The variability in the male genitalia in this form could be due to later interbreeding with other forms, at least partly. The origin of *P. alveus* is obscure; *P. alveus* itself may have originated as well in Europe as in Asia, although the *alveus* species complex as a whole is of European origin. For *P. alveus*, see further Chapter 3.

The last species of the *alveus* species complex to be dealt with is *P. schansiensis*. However, this form is very badly known and I give it only tentatively specific rank. It seems advisable to leave the species out of consideration at this place.

3. THE SPECIES OF *Pyrgus* IN THE PALAEARCTIC

1. *Pyrgus maculatus* Bremer et Grey

Bremer et Grey, 1853 — Schmett. N. China's: 11, pl. 3 fig. 6.

Type-locality: Peking.

Distribution (Map 1). — East Palearctic. From Chita and Stanovoy Khrebet, southward to S China (Yunnan, Kwang Si, Kwang Tung). The only species of the *Pyrgus* group in Japan.

In the northern part of the range widespread in the Amur district, but in the north-western part only known from Chita (Transbaicalia, 1 ♂, BM) and Mongolia (without exact locality, 1 ♀, BM).

Habitat. — Although the species is common, the habitat has rarely been recorded. According to Kurentsov (1949) in Primorsky Kraj (Maritime district) (N of Vladivostok) along river-banks and roads. From lowlands up to 1550 m (Tai Shan, prov. Shantung, China; BM), ssp. *thibetanus* to 2800 m (Ta Tsien Lou; BM), and perhaps, much higher.

Biology. — Presumably bivoltine, as morphologically two broods can be distinguished (see below), the first brood flying from March to May and the second from May to July; possibly at high altitudes and in the north a single brood, at least summer specimens from E Siberia are scarce. Kurentsov (1949) records the flight period north of Vladivostok as May-June.

The larvae have been found by Graeser on *Rubus idaeus* and *Spiraea* (Rosaceae) (Staudinger, 1892), on leaves which had been spun together.

Geographic variation. — The geographic variation of this species has long been obscured by seasonal variation. Leech (1894) divided the forms *maculatus*, *zona*, *albistrigus* and *thibetanus*, here considered conspecific, into three species and placed *albistrigus* as a variety of *zona*. All four forms were given specific rank by Warren (1926). Evans (1949) was the first to recognize the seasonal variation, perhaps he was also the first who could study an adequate number of specimens. I have seen all the material Evans studied and can only follow his classification.

Pyrgus maculatus maculatus Bremer et Grey

Pl. 1 Fig. 1—3; Pl. 2 Fig. 25—27

Material examined. — 145 ♂ 95 ♀: spring form; 1 ♂ Chita (BM), 30 ♂ 33 ♀ E Siberia (Amur, Sichote Alin, Stanovoy Khrebet, "E Siberia") (BM, ML, RJ), 10 ♂ 1 ♀ Askold (BM), 1 ♂ 2 ♀ Manchuria (BM), 1 ♂ N Korea (Seishin) (ML), 5 ♂ 1 ♀ N China, 1 ♂ 1 ♀ Peking, 3 ♂ 1 ♀ Shan Si, 1 ♂ 1 ♀ S Shen Si, 4 ♂ 4 ♀ Shantung, 9 ♂ 4 ♀ Kuku-Nor (all BM), 20 ♂ 15 ♀ Japan (BM, ML, ZMA,

RJ); summer form: 1 ♀ Mongolia, 1 ♂ 3 ♀ E Siberia, 1 ♀ Manchuria, 8 ♂ 5 ♀ Korea, 7 ♂ 2 ♀ N China, 2 ♂ Pekin, 1 ♂ 1 ♀ Shan Si, 11 ♂ 5 ♀ Shantung (all BM), 29 ♂ 14 ♀ Japan (BM, RJ).

Distribution. — The northern part of the distribution area of the species; the southern limit is not exactly known, somewhere between the Huang-ho and the Yang-tse-Kiang; there may be a wide transitional zone with ssp. *bocki*.

Subspecific characters. — Unf apex beyond the sub-apical spots uniformly coloured. Uph submarginal band of spots (only present in spring form) more or less angulated in spaces 4—5. Male genitalia: style short and broad, not nearly reaching the end of the cuiller; lamina transversa of lateral apophyses with short spines.

Two easily separable seasonal forms. Spring form: Above, with large spots, uph with conspicuous discal and submarginal spots; unh ground colour usually chestnut, submarginal spots forming a narrow, more or less continuous band, a very narrow white spot mid space 7 (sometimes absent). ♂ 12.8—14 mm. The holotype of the species belongs to this form. Summer form: Above, spots reduced, especially uph, where only two (or rarely three) central spots are present; unh ground colour more greyish dark brown, submarginal spots absent. This form was named *zona* by Mabille (1875) and being, of course, sympatric with *maculatus*, has, for a long time, been considered a separate species.

Variation. — There exists some variation in the extension of the spots above, and in the ground colour and extension of the white submarginal band unh. Some specimens from China can be separated only with difficulty from the following subspecies.

***Pyrgus maculatus bocki* Oberthür**

Pl. 1 Fig. 5—7; Pl. 2 Fig. 29—31

Oberthür, 1912 — Ét. Léop. Comp. 6: 71, figs. 1235, 1236.

Type-locality: Kiang Si.

Material examined. — 63 ♂ 42 ♀: spring form: 3 ♂ 3 ♀ Leou Fang, 3 ♂ 3 ♀ Shanghai, 3 ♂ 3 ♀ Chekiang, 6 ♂ 1 ♀ Szechwan (Chia Ting Fu), 8 ♂ 7 ♀ Hupeh, 1 ♂ 2 ♀ Fukien, 3 ♂ Kiang Si, 1 ♂ Kwang Si; summer form: 5 ♂ Leou Fang, 2 ♂ 4 ♀ Shanghai, 4 ♂ 1 ♀ Chusan Island, 1 ♂ 4 ♀ Ya Chiao Ling, 4 ♂ 1 ♀ Chekiang, 4 ♂ 1 ♀ Szechwan (Chia Ting Fu), 7 ♂ 4 ♀ Hupeh, 3 ♂ 4 ♀ Fukien, 2 ♂ Hunan, 2 ♂ 4 ♀ Kiang Si, 1 ♂ Kwang Tung (all BM).

Distribution. — The southern part of the distribution area of the species; for the northern limit, see under subspecies *maculatus*.

Subspecific characters. — Very much like subspecies *maculatus*, but differing in the spring form by a darker ground colour unh and by the absence of the submarginal band and the small spot mid space 7 unh, and in the summer form by, usually four, discal spots uph and the light greyish colour of the basal two-thirds of the hind wing below, where the small spot mid space 7 may be present.

Variation. — Varies somewhat in the extension of the white spots above (particularly uph) and in the colour unh. Some specimens of northern localities (Chekiang, Hupeh) resemble ssp. *maculatus*.

Pyrgus maculatus thibetanus Oberthür

Pl. 1 Fig. 4, 8; Pl. 2 Fig. 28, 32

Oberthür, 1891 — *Ét. d'Entom.* 15: 20; pl. 3 fig. 27.

Type-locality: Ta Tsien Lou.

Material examined. — 36 ♂ 26 ♀: spring form: 25 ♂ 9 ♀ Szechwan (Ta Tsien Lou, Wa Ssu Kow, Maenia, Batang, Quase), 9 ♂ 16 ♀ Yunnan (Li-Kiang, Tsekou, Ta Pin Tze, Teng Yuch Ting): summer form: 2 ♂ 1 ♀ Szechwan (Mosy mien, Ta Tsien Lou) (all BM).

Distribution. — SW China.

Subspecific characters. — Unf apex beyond the sub-apical spots, inner half dark, outer half white. Uph band of submarginal spots not elbowed. Male genitalia: style longer, reaching end of cuiller; lamina transversa with long spine-like hairs on either side of the aedeagus.

The difference between the spring form and the very few specimens known of the summer form is slight. Above, both forms resemble the forms of ssp. *bocki*, below they look like a pale summer form of ssp. *maculatus*, but the discal band unf is usually wider and the termen unf is broadly pale.

Geographic history. — The apparent constancy of both ssp. *maculatus* and ssp. *bocki* throughout their range clearly points to an origin of both subspecies in isolated areas, situated in N China-Manchuria and S China, south of the Yang-tse-Kiang. The cause of this separation is, however, not clear. A marine transgression could possibly inundate a large part of eastern China and the lower Yang-tse-Kiang, and cause a separation in this way.

Ssp. *thibetanus* may be older, as it differs externally as well as in the male genital armature. Presumably it is a high altitude insect, but the data are very scanty. Its range offers many possibilities for isolation by high peaks and deep valleys.

2. *Pyrgus bieti* OberthürOberthür, 1886 — *Ét. d'Entom.* 11: 26, pl. 6 fig. 50.

Type-locality: Ta Tsien Lou.

Distribution (Map 2). — Only known from the Chinese provinces Szechwan and Yunnan. For exact localities, see below. The specimens recorded by Leech (1894) from Amdo and Nan Shan probably belong to *P. dejeani*.

Habitat. — Not recorded. Undoubtedly an insect of high altitudes. The lowest altitude probably is Tse-kou (Yunnan), at 1993 m (Oberthür, 1912).

Biology. — Unknown.

Geographic variation. — Although there seems to be some overlap in the characters, there is a slight difference between the specimens from Yunnan and from Szechwan. It is difficult to evaluate this difference, as most (76 %) of the specimens studied originate from one locality, Ta Tsien Lou. However, the possibility of getting more material for study appears rather remote at the moment. So we must feel satisfied for the present with the division into two subspecies.

***Pyrgus bieti bieti* Oberthür**

Pl. 1 Fig. 9—10; Pl. 2 Fig. 33—34

Material examined. — 83 ♂ 51 ♀ : 67 ♂ 49 ♀ Ta Tsien Lou (BM, ML), 7 ♂ Wa Ssu Kow, 6 ♂ 1 ♀ Yaragong, 1 ♂ Vrianotsang, 1 ♂ Batang, 1 ♀ Rama La (SE Thibet), 1 ♂ Maenia (all BM).

Distribution. — W Szechwan.

Subspecific characters. — Unh ground colour greenish to ochreous, submarginal white spots in spaces 1-c and 2 extend to termen, discal white band narrower than in ssp. *yunnanus*.

Variation. — The ground colour unh may be as reddish as in ssp. *yunnanus* and sometimes the submarginal spots in spaces 1c and 2 are separated from the termen by traces of dark dots. There is also some variation in the width of the discal band unh and in the extension of the spots above.

There is an obvious sexual dimorphism, males being much more distinctly marked than females.

***Pyrgus bieti yunnanus* Oberthür**

Pl. 1 Fig. 11—12; Pl. 2 Fig. 35—36

Oberthür, 1912 — Ét. Léop. Comp. 6:66.

Type-locality: Yunnan.

Material examined. — 14 ♂ 5 ♀ Yunnan (Li-kiang, Ta Pin Tze) (BM).

Distribution. — N Yunnan.

Subspecific characters. — Unh ground colour generally redder than in ssp. *bieti*, submarginal spots in spaces 1-c and 2 separated from termen by dark spots, discal band wider than in ssp. *bieti*.

Variation. — The specimens examined varied in all characters, some specimens were almost inseparable from ssp. *bieti*.

Sexual dimorphism as in ssp. *bieti*.

Geographic history. — With the present data it is impossible to get a clear picture of the history of the species. Evidently, the separation into subspecies is very young. The extreme differences in altitude in the distributional area, caused by the steep and deep river valleys, offer many possibilities for isolation. As *P. bieti* presumably is an insect of high altitude, an amelioration rather than a worsening of the climate may cause isolation. It is, therefore, not impossible that the differentiation observed is of postglacial age.

3. *Pyrgus oberthuri* Leech

Leech, 1891 (June) — Entomologist 24, suppl.: 59.

Type-locality: Wa Ssu Kow.

Distribution (Map 3). — The Chinese provinces Szechwan and Yunnan. One male is known from Fort Naryn (E Turkestan) (BM).

Habitat. — Not recorded. Undoubtedly a species of high altitudes, as *P. bieti*. At least to 4000 m (Wushi, Szechwan) (BM).

Biology. — Unknown.

Geographic variation. — Two subspecies can be distinguished which differ in the male genital armature and the colour unh.

Pyrgus oberthuri oberthuri Leech

Pl. 1 Fig. 13—14; Pl. 2 Fig. 37—38

Material examined. — 27 ♂ 9 ♀: 16 ♂ 3 ♀ Ta Tsien Lou, 9 ♂ 6 ♀ Wa Ssu Kow, 1 ♂ Batang, 1 ♂ Fort Naryn (E Turkestan) (all BM).

Distribution. — SW China, E Turkestan.

Subspecific characters. — Unh ground colour dark greenish brown. Male genitalia: apex of cuiller more rounded.

Note. — According to Evans (1949) smaller than ssp. *delavayi*, ♂ 13—14 mm, but some males (Ta Tsien Lou) are as large as ssp. *delavayi*, 16 mm, and therefore, size cannot be considered an important subspecific character.

Pyrgus oberthuri delavayi Oberthür

Oberthür, 1891 (July) — Ét. d'Entom. 15: 20; pl. 3 fig. 31.

Type-locality: Yunnan.

Material examined. — 47 ♂ 2 ♀: 33 ♂ 1 ♀ (Szechwan, Wushi 12000 ft), 14 ♂ 1 ♀ Yunnan (Teng Yueh Ting, Ta Pin Tze, Li-kiang) (all BM).

Distribution. — SW China.

Subspecific characters. — Unh ground colour generally light greenish grey-brown by white or creamish superscaling, except narrow dark brown lines along white spots. Male genitalia: Apex of cuiller more pointed.

Note. — (1) The characters only refer to the males, as only two females are known. Moreover, the female from Wushi has a reddish unh. (2) According to Picard (1948b) there is a single geographic form, but he only refers to figures of Leech and Oberthür and evidently, he did not study much material.

Geographic history. — Presumably this species has a history parallel to that of *P. bieti*. Although it seems to have a much wider distribution, it is nevertheless senseless to speculate on the history on the base of the single male known from Turkestan.

4. *Pyrgus dejeani* Oberthür

Oberthür, 1912 — Ét. Léop. Comp. 6: 66—67.

Type-locality: Ta Tsien Lou.

Distribution (Map 4). — Only known from Tibet, Sikkim and W Szechwan. Furthermore, one male and one female are known from Tura (BM). According to Evans (1949) this locality is in Transcaspian, but according to Warren (1936) it is in the Namangan district in Ferghana. As far as I know, most specimens labeled "Tura" came from Staudinger, who explained "Tura" (in Staudinger - Rebel, 1901) to be the

Achal Tekke region in Transcaspien. Therefore I think that Evans is right. Apparently it is a rare insect, but it may be widely distributed in Tibet.

Habitat. — Not recorded. In Sikkim at 4000 m (BM).

Biology. — Unknown.

Geographic variation. — There is some variation in size, ♂ from 12.4 to 14.7 mm. The larger specimens are from Ta Tsien Lou. Other variations are unknown, probably because of the scarcity of the material. (Pl. 1 Fig. 15—16; Pl. 2 Fig. 39—40).

Material examined. — 13 ♂ 13 ♀ : 6 ♂ 5 ♀ N Tibet (Amdo, Nan Shan), 2 ♂ 2 ♀ SE Tibet (Charme, Gyantse, Pusho, Kyari Dzong), 1 ♀ E Tibet (Nenden), 3 ♂ 3 ♀ W Szechwan (Ta Tsien Lou), 1 ♂ 1 ♀ Sikkim (Chumbi Valley, 12,000 ft), 1 ♂ 1 ♀ Tura (all BM).

5. *Pyrgus carthami* Hübner

Hübner, 1808—1813 — Samml. europ. Schmetterl. 1: pl. 143 fig. 720—723.

Type-locality: S Germany (selection by Alberti, 1938).

Nomenclature. — There is little uniformity in the use of the specific name of this species: both the names *carthami* Hübner, 1809—1813 and *fritillarius* Poda, 1761, are in use. The difficulties arise from the interpretation of the original description of *fritillarius* and from the interpretation of the figure referred to by Poda. About *carthami* there has never been any difference of opinion, so I prefer to use the name *carthami*, thus following Lempke (1953) and Alberti (1952-c, 1953-b).

Distribution (Map 5). — West Palaearctic: from Spain to E Russia and S Turkestan; even known from Saisan. In Spain wide-spread, from Andalusia to the Pyrenees. Undoubtedly the species also occurs in Portugal, but I have not found any record of this; it is not recorded by Zerkowitz (1946), nor by Da Silva Cruz (in litt.). Practically throughout France and throughout C and S Europe. Not in Corsica and Sardinia (Verity, 1940), the northwestern part of Switzerland (Kauffmann, 1951) and the northwestern part of peninsular Italy (Verity, 1940). No reliable records from the Peloponnesus. The northern limit roughly runs from the mouth of the Loire through SE Belgium to Stettin and Danzig (Friese, 1956). Once collected in the Netherlands (Lempke, 1953). Farther east the most northern localities are Wolmar (Petersen, 1924), Podolsk (BM) and Kasan (Krulikovskiy, 1908). In Siberia only known from Saisan (1 ♂, BM).

In S Russia known from the Crimea (Korshunov, 1964) and Sarepta (Eversmann, 1844; ML, BM). Not in the Caucasus (Alberti, 1969). In Turkey evidently very rare, recorded by Alberti (1938, 1969) from Konia and Taurus Mts. Farther east only recorded from Askhabad (Alberti, 1938).

Habitat. — Flowery meadows, way-sides, mountain slopes, from lowlands to 2200 m in the Alps (Verity, 1940; Kauffmann, 1951) and the Pyrenees (Caradja, 1893; Dufay, 1961); in the Sierra Nevada still common at 2500 m (Manley & Allcard, 1970).

Biology. — Monovoltine. In Switzerland flight period from the middle of May until the end of July in the valleys, and from the beginning of June to the middle of August in the mountains (Kauffmann, 1951). Records of two broods per year (e.g. Caradja, 1893; Manley & Allcard, 1970) are presumably biased by the long flight period.

Various plant species have been recorded as food plants; presumably some of them are false, but this is difficult to prove. Most records undoubtedly do not rely on own observations. I think the following summary is complete as far as the recorded food plants are concerned.

Malvaceae: *Althaea*, *A. officinalis*, *A. hirsuta* (Verity, 1940; Schmidlin, 1948; Forster & Wohlfart, 1955; Manley & Allcard, 1970; Higgins & Riley, 1970); *Malva*, *M. sylvestris* (Verity, l.c.; Schmidlin, l.c.; Forster & Wohlfahrt, l.c.; Manley & Allcard, l.c.); *Carthamus lanatus* and *coeruleus* (Guillaumin, 1964).

Rosaceae: *Potentilla*, *P. opaca*, *P. verna* (Bergmann, 1952; Friese, 1956; Higgins & Riley, l.c.).

Compositae: *Centaurea* (Verity, l.c.; Schmidlin, l.c.; Manley & Allcard, l.c.).

Gramineae: (Schmidlin, l.c.; Guillaumin, l.c.).

Geographic variation. — A highly variable species of which many forms have been described as subspecies. As is mostly the case when subspecies are distinguished for the sake of the distinction, the splitting-up has obscured the pattern of geographic variation, rather than cleared the picture. Alberti (1938) was the only one who studied the geographic variation throughout the range of the species. Although he evidently had too little material available from Spain and France, his conclusions are very valuable, as he looked for the relations between the subspecies. The treatment of the geographic variation by Evans (1949) is inadequate; he only recognized the subspecies *carthami* and *moeschleri*, which as will be shown below, do not represent the geographic variation very well.

The variation comprises the following characters: size, extension of white spots above, extension of white spots unh, extension of white superscaling above and unf, colour and extension of the dark areas unh. Presumably, these characters are greatly influenced by climatic conditions. It is therefore not necessary to assume in advance a historic relation between forms that are of the same size, that have the same white superscaling, etc. The relations supposed below are, at any rate, historically understandable.

nevadensis subspecies group

The position of ssp. *nevadensis* from the Sierra Nevada has long remained obscure, due to lack of material. Neither Warren (1926), nor Alberti (1938) had seen this subspecies. While he had only two specimens from the Sierra Nevada available for comparison, Zerny (1927a) classified also specimens from Albarracín (C Spain) as this subspecies. As a result the variation of the species in Spain remained unclear and herewith also the position of the forms outside Spain.

The group is characterized by the pale yellow ground colour unh. This colour can be almost white (*nemausensis*) but is usually overlaid by dark scales, especially around the white spots. In this way lighter and darker patches are formed. In specimens from the Pyrenees the darkening is usually more uniform. Size usually medium to small, in some cases very large. Extension of white spots and light superscaling above very variable. Unf usually light grey.

The group has a vast distribution, but the northern and eastern limits are very unsharp, owing to intergradation with other subspecies groups. The distribution comprises Spain, France and peninsular Italy. The transition to the *carthami* subspecies group is very gradual. The greater part of E France should probably be considered a transitional zone, as the influence of the *carthami* subspecies group is clearly perceptible in SE France (Basses Alpes) and even in peninsular Italy, while the influence of the *nevadensis* subspecies group can be traced in many German specimens. Such transitional populations are historically easily understandable, but they cannot be classified. I regard all French

populations as belonging to the *nevadensis* group only for practical reasons. In N Italy the influence of the *valesiacus* subspecies group is perceptible in some specimens from the Ligurian Alps (by the size and the colour unh). Farther east, the populations of the southern Alps show only *valesiacus* characters. Only rare specimens (e.g. Naturns, Feltre) recall the *nevadensis* subspecies group. According to Verity (1940) specimens transitional between ssp. *valesiacus* and ssp. "*carthami*" occur in the Turin district. Four subspecies have been described within the *nevadensis* subspecies group. They only comprise a part of the total variation of the group. The remainder of the variation will be discussed after the four subspecies. Further research will possibly indicate, that the *nevadensis* subspecies group constitutes one single subspecies.

Pyrgus carthami nevadensis Oberthür

Pl. 3 Fig. 37, 46

Oberthür, 1910 — Ét. Léop. Comp. 4: 384; pl. 55 fig. 474.

Type-locality: Sierra Nevada.

Material examined. — 30 ♂ 11 ♀ Sierra Nevada (BM, ZMA, HC).

Distribution. — Sierra Nevada.

Subspecific characters. — Size moderate, ♂ 14–16 mm. Upf spots large, little white superscaling. Uph spots usually well developed, especially the submarginal spots; central band often vague. Unf dark to light grey. Unh spots well developed, especially the central spot; spots bordered by dark brown lines; the darkening of the very light yellow ground colour variable, but not extending over more than half of the ground colour.

Note. — Oberthür (1910), naming this subspecies, quoted the description of Rambur (1858) who stated that the specimens from the Sierra Nevada differ from French specimens, e.g. "par le dessous des ailes inférieures, dont la bord externe présente une nuance d'un roussâtre obscur, mais ne s'unissant pas complètement avec le dessin des ailes comme chez l'*Alveus*" (p. 67). I do not exactly follow the meaning of this, at any rate I did not observe a reddish termen.

Pyrgus carthami pyrenaicus Warren

Pl. 3 Fig. 38, 47

Warren, 1926 — Trans. ent. Soc. Lond. 74: 69.

Type-locality: Pyrenees.

Nomenclature. — Verity (1928) thought it necessary to replace the name *pyrenaicus* by *microcarthami* as Tutt (1906) had given the name *pyrenaica* to a form of *P. malvoides*. This was not a subspecific name and therefore it is not necessary to replace Warren's name (see also under *P. malvoides*).

Material examined. — 51 ♂ 24 ♀: 12 ♂ 9 ♀ Spanish Pyrenees (prov. Huesca) (RJ), 27 ♂ 5 ♀ Hautes Pyrénées (BM, ML, ZMA, RJ), 12 ♂ 10 ♀ Pyrénées Orientales (BM, ML, ZMA).

Distribution. — Confined to the Pyrenees.

Subspecific characters. — The most important character is the small size, ♂ 13–14.5 mm. Above, spots medium-sized, on hindwing often obscure, light suffusion slight or

wanting; unh ground colour sometimes rather uniformly darkened, spots variable but usually not as wide as in ssp. *nevadensis*.

Variation. — This subspecies seems to be most constant in the Central Pyrenees (at both the Spanish and the French sides), and even there some specimens cannot be separated from those from C France or C Spain. In the Eastern Pyrenees larger specimens increase in number, giving this region the character of a transitional zone. Three males examined, from the Spanish side (prov. Gerona), were indistinguishable in size (14.8—15.2 mm) and in light superscaling, from specimens in C Spain. Therefore, I did not include these specimens within ssp. *pyrenaicus*.

Pyrgus carthami lucasi Reverdin

Reverdin, 1928 — Bull. Soc. Léop. Genève 6: 91—92; pl. 2 fig. 5 and 6.

Type-locality: Forêt de Benon.

Material examined. — 4 ♂ 4 ♀ Forêt de Benon (ML).

Distribution. — According to Picard (1948c), it is the race of the "plaines atlantiques".

Subspecific characters. — According to the original description it only differs constantly from ssp. *pyrenaicus* by the presence of small white streaks in the dark ground colour unf between the veins, beyond the median spots. However, Alberti (1938) showed that the choice of this character is not very fortunate, as the white streaks are present in many other forms.

Although I studied a limited number of specimens, I cannot consider the combination of small size and very light ground colour unh the most important character, as stated by Alberti (l.c.). The specimens examined show very well the characters mentioned by Picard (1948c): reduction of the dark lines surrounding the ground colour unh, the ground colour varying from vivid yellow orange to pale yellow. Sizes, measured by me, were: ♂ 11.5, 13.6, 13.8, 14.0 mm, ♀ 13.2, 14.8, 15.0, 15.1 mm.

Note. — The vivid yellow-orange ground colour unh may indicate influence of the *carthami* subspecies group.

Pyrgus carthami nemausensis Picard

Picard, 1948 — Lambillionea 48: 28—29.

Type-locality: Nîmes.

Material examined. — None.

Distribution. — According to Picard, confined to the rifle-range of Nîmes.

Subspecific characters. — A very pale form; above not only a rather strong suffusion with white scales, but the normal brown-black tinge is also very bleached; ground colour unh very light: in the female only yellowish patches have been left, in the male the ground colour is white with only traces of the dark lines around the spots. Even these traces may disappear, making the unh unicoloured white (Picard named this form *deficiens*). Somewhat smaller than the form of C France, with narrower wings.

Note. — This form is an extreme of the variation which may be found throughout the range of the *nevadensis* subspecies group, especially in Spain and S France. I have studied specimens from Albarracin (C Spain) and Digne (SE France) which show the same characters, although not in an equally extreme way.

I doubt the usefulness of distinguishing subspecies when they are only based on an extreme variation and, moreover, have a very limited distributional area. The rifle-range of Nîmes is a dry and hot locality. Perhaps the extreme environmental conditions have caused the extreme variation. In this connection it is useful to quote the case of the hesperiid *Ochlodes venatum concoulense* Picard. Picard (1948-c) distinguished this subspecies on account of a series of specimens captured in three successive years at a rather wet locality in S France (Mont Lozère), while everywhere in the surroundings the subspecies *septentrionale* was flying. According to Gaillard (1952) the subspecies (sic!) *concoulense* had lost its characters after three years of drought and had become *septentrionale*! (see also Chapter 1.b).

Remainder of the *nevadensis* subspecies group

The remainder of the local variation within the *nevadensis* subspecies group has not yet been named. The name *carthami* has been used by most authors to cover this remainder variation. Alberti (1938) selected S Germany as the type locality of the species. However, in my opinion another subspecies group occurs in S Germany, viz. *carthami* subspecies group; so, it is impossible to use the name *carthami* as a subspecific name in the *nevadensis* subspecies group. It should be noted that some specimens from S Germany are inseparable from French, or even Spanish or Italian specimens. This is only to be expected, as in E France and S Germany the *nevadensis* and *carthami* subspecies groups are mixed. In Spain the variation of the *nevadensis* group is large. In size the specimens vary from *pyrenaicus* to *nevadensis*, but as already noted by Alberti (1938), very large specimens occur in the Sierra de Gredos; I saw a male from Navarredonde in the Sierra de Gredos of 16.5 mm and a female of 17.4 mm! (ZMA). Many specimens from Albarracín are very strongly suffused with white scales above, some are darker and a few are as dark as ssp. *nevadensis*, without reaching the same extension of the white spots. At nearby Cuenca some specimens are almost inseparable from specimens taken in the Sierra Nevada.

In France the specimens are less variable, 13—15.5 mm, with usually an obvious white suffusion above. The white spots above are well-developed but not large and they are often faintly visible on the hind wing, in particular the median spots. Some specimens from the Basses Alpes and the Alpes Maritimes look like specimens from Albarracín, but in the same region the dark suffusion of the hind wing below may cover almost all the pale yellow ground colour. This ground colour is rather vivid yellow in some specimens, indicating the influence of the *carthami* subspecies group.

In Italy the variation is about the same as in Spain, but I have not seen such large specimens as from the Sierra de Gredos. In the Abruzzi most specimens are inseparable from specimens taken in C Spain (including Albarracín). Specimens from Calabria are rather large (up to 16.2 mm) and dark above, due to reduction of white spots and scanty of white superscaling.

The only known specimen from the Netherlands, a male of 13.9 mm, was listed by Lempke (1953) as ssp. *septentrionalis*, but in my opinion it belongs to the *nevadensis* subspecies group.

Material examined. — 242 ♂ 132 ♀: 59 ♂ 32 ♀ Spain (Andalusia to Gerona) (BM, ML, ZMA, HC, RJ), 151 ♂ 80 ♀ France (Pyrenees to Alps and to Fontainebleau) (BM, ML, ZMA, HC, RJ), 1 ♂ Belgium (Virton) (ML), 1 ♂ Netherlands (De Lutte) (ML), 29 ♂ 20 ♀ C and S Italy (BM, ML, ZMA, RJ), 1 ♂ Sicily (BM).

valesiacus subspecies group

A well-defined group of medium-sized to large forms, occurring in the southern Alps and southward to Bosnia and, largely separated, in N Germany. Above, light suffusion generally scarce or absent, giving the specimens a dark appearance. Spots uph usually faintly developed, in some specimens absent. Ground colour unh dark.

Three subspecies can be distinguished.

***Pyrgus carthami valesiacus* Mabille**

Pl. 3 Fig. 40—41, 49—50

Mabille, 1876 — Bull. Soc. Ent. France (5) 5: 214.

Type-locality: Valais.

Material examined. — 90 ♂ 44 ♀ : 26 ♂ 13 ♀ Switzerland (Valais) (BM, ML, ZMA), 62 ♂ 31 ♀ N Italy (Val d'Aosta to Trentino and prov. Udine) (BM, ML, ZMA, RJ, HO), 2 ♂ Austria (Landeck) (RJ).

Distribution. — Southern Alps, not at the French side.

Subspecific characters. — Large, ♂ to 16.8 mm. Above, white suffusion absent (typical form) or obvious (f. *major* Rebel). Upf spots well developed, uph spots faint or wanting. Unh ground colour a pale shade of yellow, but darker than in the *nevadensis* subspecies group, with strong dark superscaling, giving the colour a dirty yellow-green tinge with or without light patches. Unf black with sharply contrasting white spots. There is a strong intermingling with ssp. *carthami* in Valais as stated by Verity (1940) and Kauffmann (1951) (perhaps also with influence of the *nevadensis* subspecies group). To the north and to the east the transition to ssp. *carthami* seems rather rapid. The most northern locality from which I have seen ssp. *valesiacus* is Landeck in W Austria. Eastward from the Gross Glockner all Austrian populations seem to belong to ssp. *carthami*.

According to Kauffmann (1951) the occurrence and relative abundance of f. *major* depend on micro-climate and weather conditions during the year.

***Pyrgus carthami analogus* Alberti**

Pl. 3 Fig. 39, 48

Alberti, 1938 — Stett. ent. Zeit. 99: 244.

Type-locality: Trebevic, Sarajevo.

Material examined. — 63 ♂ 6 ♀ : 21 ♂ Croatia (BM), 42 ♂ 6 ♀ Bosnia (Trebevic) (BM, ZMA, RJ).

Distribution. — Yugoslavian mountains; southern limit unknown.

Subspecific characters. — Medium-sized, ♂ 1.4—1.6 mm. On the upperside, this form looks like ssp. *valesiacus*; uph spots often rather well-developed. Unh spots reduced, especially the central spot, which almost always lacks the projection towards the base of the wing; ground colour rather dark yellow, in most cases evenly overlaid by dark scales, usually a warmer tinge than in ssp. *valesiacus*. The colour and reduction of spots unh give the form an appearance that recalls *P. serratulae balcanicus*.

Note. — The populations from Croatia can best be listed as this subspecies, although they show the influence of the neighbourhood of ssp. *valesiacus* and ssp. *carthami*.

***Pyrgus carthami septentrionalis* Alberti**

Pl. 3 Fig. 42, 51

Alberti, 1938 — Stett. ent. Zeit. 99: 236—237.

Type-locality: Neumark (Bärwalde).

Material examined. — 4 ♂ 3 ♀ Berlin and environments (BM, ML, RJ), 1 ♂ Livonia (BM).

Distribution. — From Berlin north and north-east to the Baltic.

Subspecific characters. — As large as ssp. *valesiacus* or slightly larger. Upperside white suffusion very scanty; spots somewhat reduced as compared to ssp. *valesiacus*; spots uph small but obvious. Unh dark grey-greenish, sometimes brownish, without light patches; dark colour almost to the termen, white spots strongly contrasting, isolated but well developed.

The specimens enumerated above agree well with Alberti's description.

***carthami* subspecies group**

Size medium to large, usually with well-developed white spots on both fore and hind wings, light superscaling variable, usually well marked, rarely absent; ground colour unh usually yellow to vivid orange-yellow, rarely as pale as in the *nevadensis* subspecies group; dark suffusion brown, variable, but rarely covering all the ground colour of the hind wing and not sharply outlining the white spots as in the *nevadensis* subspecies group.

This group is widely distributed in E Europe, but occurs as far west as W Germany; see also under the *nevadensis* subspecies group.

***Pyrgus carthami carthami* Hübner**

Pl. 3 Fig. 43—44, 52—53

Material examined. — 101 ♂ 60 ♀: 29 ♂ 12 ♀ Germany (Bavaria to Mainz) (BM, ML, RJ), 14 ♂ 13 ♀ Switzerland (excl. Valais) (BM, ML), 27 ♂ 18 ♀ Austria (eastward from Gross Glockner) (BM, ML, RJ), 15 ♂ 11 ♀ Hungary (BM, ML, ZMA, RJ), 1 ♂ 1 ♀ Czecho-Slovakia (BM), 14 ♂ 5 ♀ Rumania (BM, RJ), 1 ♂ Bulgaria (BM).

Distribution. — From N Switzerland and W Germany through C and E Europe. The eastern limit is unknown. Some Hungarian specimens cannot be separated from ssp. *moeschleri*.

Subspecific characters. — ♂ 14—16.1 mm. Differs from the only other subspecies of the group by its smaller size and less developed spots above, especially on hind wing.

Variation. — In S Germany and Switzerland and, very rarely, in Austria, some specimens have a pale yellow unh as in the *nevadensis* subspecies group. To the east the specimens vary towards ssp. *moeschleri*.

***Pyrgus carthami moeschleri* Herrich-Schäffer**

Pl. 3 Fig. 45, 54

Herrich-Schäffer, 1854 — Syst. Schmett. Eur. 6: 175.

Type-locality: designated hereby Sarepta.

Material examined. — 33 ♂ 21 ♀: 29 ♂ 18 ♀ Sarepta (BM, ML), 1 ♂ 1 ♀

Guberli (BM), 1 ♂ 1 ♀ Kisilskaja (RJ), 1 ♂ Saisan (BM), 1 ♂ Urumi (BM), 1 ♀ "Broussa" (BM).

Distribution. — SE Russia, SW Siberia; according to Alberti (1938) the same form occurs at Askhabad.

Subspecific characters. — Large, ♂ 15.4–17 mm. Upperside, spots large, light suffusion obvious; uph median band conspicuous and even one or two basal spots obvious; upf obvious submarginal light streaks between the veins.

Geographic history. — The outline of the history of the species from the Last Glacial to the present appears little complex. We may assume three or four refugial areas for this species during the Last Glacial: (1) Spain, (2) N Italy - S Alps, (3) SE Europe and, possibly separated from (3), (4) S Russia.

From Spain the *nevadensis* subspecies group spread postglacially far to the north, but in E France it met *carthami* which spread westward from a SE European refugium, possibly through the valley of the Danube. By this expansion ssp. *carthami* cut off the northward expansion of the *valesiacus* subspecies group from its refugium in the southern Alps. Alberti (1938) may be correct in supposing (indirectly) that the *valesiacus* subspecies group was adapted to less favourable climates than the *carthami* subspecies group, thus making the discontinuous distribution of the *valesiacus* subspecies group understandable. In its south-eastward extension the *valesiacus* subspecies group came into contact with ssp. *carthami*. The result of this contact can be seen in ssp. *analogus* in the smaller size and the warmer tinge of the ground colour unh, as compared to ssp. *valesiacus*.

Ssp. *carthami* and ssp. *moeschleri*, though closely related, may have had separate refugial areas. Material from SW Russia probably could elucidate this point.

The history of the species before the Last Glacial cannot be reconstructed on the ground of the present data.

6. *Pyrgus sidae* Esper

Esper, 1782 — Eur. Schmett. 1, 2: 178, pl. 90 fig. 3.

Type-locality: Volga region.

Distribution (Map 6). — Southern Palaearctic, from S France to Turkestan.

In France only known in the south, in the départements Hérault, Gard, Bouches-du-Rhône, Var, Alpes Maritimes and Basses Alpes (Verity, 1947; Picard, 1948c; Gaillard, 1952; see also below, sub "Material examined"). In Italy widely distributed from Liguria to the Monti Aurunci and from N Italy recorded from several localities in the northeast (Verity, 1940).

From Hungary through the Balkans and Turkey to Turkestan, perhaps not continuously (a.o. Caradja, 1895; Bachmetjev, 1902; Rebel, 1903, 1904, 1913; Thurner, 1964; Groum-Grshimailo, 1890). In Iran only known from two specimens in the BM labelled "Persia". See also below, Material examined. Widely distributed in Transcaucasia, but from the Caucasus only known from Teberda and Itkol (Romanoff, 1884; Alberti 1969). In Russia from Taganrog (Alpheraky, 1908) to the southern Urals (Eversmann, 1844). Recorded by Lederer (1853) from the Irtisch River between Ustkamenogorsk and Ustbuchtarminsk. This is the most eastern record of the species, but it possibly concerns *Syrictus antonia* and for that reason I consider the record unreliable.

Habitat. — Dry and open, flowery places. Most common at low altitudes, particularly in France and Italy (Warren, 1926; Verity, 1940), but in SE Europe to 2000 m (own observation), likewise in the Caucasus at Itkol (Elbrus) (Alberti, 1969), and in Turkestan to 2700 m (Ugam Valley) (BM).

Biology. — Monovoltine; flight period from the middle of May to the end of July, depending on altitude and local conditions. According to Guillaumin (1964) the larvae have been found on *Abutilon avicennae* (Malvaceae).

Geographic variation. — There is a marked geographic variation in size, colour and design and it is not difficult to distinguish three subspecies. However, the subspecific classification of specimens from Central Asia is unsatisfactory.

Pyrgus sidae occiduus Verity

Pl. 4 Fig. 55—56, 64—65

Verity, 1925 — Ent. Rec. 37: 76.

Type-locality: Tuscany.

Material examined. — 88 ♂ 54 ♀ : 62 ♂ 30 ♀ France (Hérault, Bouches-du-Rhône, Var, Alpes Marit., Basses Alpes) (BM, ML, MP, RJ), 26 ♂ 24 ♀ Italy (Firenze, Monti Aurunci, Monti Meta, "Italy") (BM, ML).

Distribution. — S France and Italy. For details of the distribution, see under the distribution of the species.

Subspecific characters. — Generally smaller, ♂ (and ♀) 14—15.5 mm, but much variation exists and there is a great overlap with the other subspecies. The smallest specimen I have seen is a male from S France with a fore wing length of only 12.8 mm, but also specimens (both ♂ and ♀) can be found of 16.6 mm or even more. Fig. 57 is based on individual measurements of 30 specimens from S France and Italy (males and females do not differ in size), which gives an impression of the difference in size with more eastern populations and of the great overlap.

There are other differences which show less overlap. The usually bright orange coloured bands unh in the nominate subspecies vary from pale yellow to pale orange in ssp. *occiduus*, rarely reaching the bright orange of ssp. *sidae*; these bands are less heavily outlined in black, more regularly formed and narrower in ssp. *occiduus*. The last-mentioned character becomes clear when we measure the width of the central spot along vein 5 and the breadth of the outer orange band along vein 5. Measured in this manner, the central spot is wider than the orange band in ssp. *occiduus*, often twice or even more times as wide; in ssp. *sidae* the central spot is, at the most, as wide as the orange band and generally it is obviously narrower.

Finally, the spots on upperside are somewhat smaller and less square than in ssp. *sidae*.

Note. — According to Evans (1949) two more or less intergrading forms exist, a small form with yellow bands and a larger form, resembling ssp. *sidae*. The variation, however, appears rather continuous and in my opinion it is undesirable to recognize two forms.

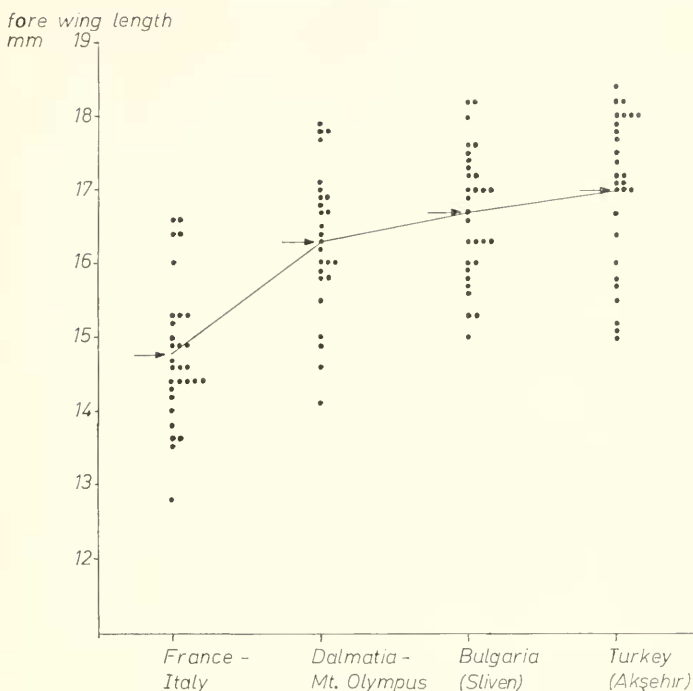


Fig. 57. *Pyrgus sidae*. Length of fore wing in four localities (regions). ● = one specimen. The line connects the mean values (arrows)

Pyrgus sidae sidae Esper

Pl. 4 Fig. 58—60, 67—69

Material examined. — 173 ♂ 70 ♀: 1 ♂ 1 ♀ Hungary (Budapest) (BM), 1 ♂ 2 ♀ Dalmatia (BM), 1 ♂ 1 ♀ Herzegovina (BM), 1 ♂ Montenegro (RJ), 37 ♂ 8 ♀ Macedonia (Yugoslavian and Greek) (BM, ML, RJ), 22 ♂ 23 ♀ Bulgaria (Rila, N Rhodope, Sliven) (BM, RJ), 15 ♂ 7 ♀ Bosphorus (BM), 60 ♂ 15 ♀ Turkey (BM, ML, RJ), 5 ♂ 1 ♀ Syria (BM), 1 ♂ 1 ♀ Iran ("Persia") (BM), 21 ♂ 9 ♀ S and E Russia (BM, ML, RJ), 2 ♂ Pamir (BM), 6 ♂ 2 ♀ Turkestan (Alexander Mts, Naryn, Ugam Valley, Semirechensk, N Tianshan) (BM, ZMA).

Distribution. — The whole distributional area of the species, except France, Italy and NE Iran.

Subspecific characters. — Larger than ssp. *occiduus*, generally 16—18 mm, with larger spots above, and bright orange bands unth that are strongly indented, broad and heavily outlined in black. See also ssp. *occiduus*.

Variation. — There is a general increase in size from west to east, Fig. 57. Apart from this, the Bulgarian specimens differ obviously from the Turkish (when observed in a series), by the smaller spots and less white superscaling above. Macedonian specimens resemble Turkish. (Pl. 4 Fig. 58—60, 67—69).

The Central Asian specimens are small, ♂ 14.4—16.4, ♀ 14.6—16.4 mm, upper-side strongly marked in both fore and hind wing, bands unh pale to deep orange, irregular, as wide as in Turkish specimens or narrower.

Pyrgus sidae evansi Alberti

Pl. 4 Fig. 57, 66

Alberti, 1957 — Mitt. Deutsch. Entom. Ges. 16: 27.

Type-locality: Arwas.

Material examined. — 3 ♂: 2 ♂ Askhabad (paratypes; BA), 1 ♂ Arwas (ML).

Distribution. — Only known from the Koppe Dagh region: Askhabad, Arwas, Nochur Tekke (Alberti, 1957).

Subspecific characters. — On the upperside the spots are well developed, but on the hind wings usually only the submarginal spots are distinct. Approximately as large as ssp. *sidae*, 15—18 mm. Underside with a dun tinge, orange bands faded yellowish, with straight sides, somewhat like ssp. *occiduus*; median band wide.

Geographic history. — The recent history of the species appears little complex. Obviously, ssp. *occiduus* originated during the Last Glacial in an Italian refugium. It is possible that in Postglacial times it came into contact with ssp. *sidae* which spread northwestward from a refugium in the Balkans and Turkey, having resulted in the great variability of ssp. *occiduus*. The variation found in ssp. *sidae* may be of postglacial age and is perhaps due to local climatic differences. From its East Mediterranean refugium ssp. *sidae* extended its range not only westward, but also northward into Russia, either along the west-side of the Black Sea, or along the Caucasus.

Presumably, the species was also isolated in a Last Glacial refugium in NE Iran (ssp. *evansi*), but the present subspecific position of the Central Asian populations is not clear. The material is insufficient to speculate on the history of the Turkestanian populations.

7. *Pyrgus badachschanus* Alberti

Alberti, 1939 — Entom. Rundschau 56: 107—109.

Type-locality: Badakhshan (Sebaktal).

Distribution. — Except from the type-locality (Sebaktal = Sebak Valley) in NE Afghanistan only known from Panjao (SW Koh-i-Baba Mts, W of Kabul) and from the upper Panjshir Valley (N of Kabul) (Wyatt & Omoto, 1966).

Habitat. — The two type specimens came from the "Alpenwiesenzone, 2800 bis 3000 m" (Alberti, l.c.). Wyatt & Omoto (l.c.) collected the species in the upper Panjshir Valley at 3800 m.

Biology. — Unknown.

Geographic variation. — Unknown.

Material examined. — 2 ♂ 1 ♀, Hindu-Kush (upper Panjshir Valley) (CW). (Pl. 1 Fig. 15, 33).

8. Superspecies *Pyrgus alpinus* Erschoff

Taxonomy. — Under the name of *Pyrgus alpinus*, Evans (1949) united three forms which, according to him, have similar genitalia. Alberti (1952a), however, pointed out that there are clear cut differences in the male genitalia, and the possibility of distributional overlap without interbreeding led him to consider the three forms separate species. Apart from some additional material I examined the same material as Evans did and can only confirm Alberti's conclusions. A distributional overlap is not yet known, but the three forms apparently approach each other very closely. The use of the term "superspecies" may indicate the supposed close relationship between these three forms or semispecies which among Palaearctic *Pyrgus* species have a unique feature in common, viz. the absence of a costal fold in the male.

The differences in the male genitalia are mainly the shape of the cuiller, the length of the style and the shape and spines of the antistyle (Fig. 58—60):

alpinus — cuiller relatively long, dorsal ridge often slightly concave; style almost reaching distal end of cuiller; antistyle elongated, blunt, slightly spined.

cashmirensis — cuiller slightly shorter, apex usually strongly spined; dorsal ridge often concave; style as long as in *alpinus*; antistyle short and broad, angular, strongly spined.

darwazicus — cuiller rounded; style short, not nearly reaching distal end of cuiller; antistyle short, but pointed, more or less spined.

As far as presently known these three types of genitalia are constant: no transitional genitalia have been found. Even in the remarkable race *cashmirensis pseudoalpinus* — externally indistinguishable from *alpinus* — the genitalia are entirely of the *cashmirensis* type.

Alberti based *pseudoalpinus* on two males from Gilgit and the Baroghil Pass (N

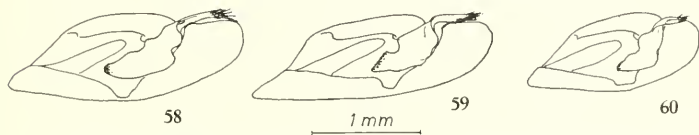


Fig. 58—60. Male genitalia of superspecies *Pyrgus alpinus*. 58, *P. alpinus* (C Asia); 59, *P. cashmirensis* (Pahalgam, NE Kashmir); 60, *P. darwazicus lilliput* (Anjuman Pass, NE Afghanistan)

Chitral) and supposed that the specimens in the BM from NW Kashmir (Hunza, Yasin, Astor, Gilgit, Chitral), identified by Evans (1949) as *alpinus*, belonged to *cashmirensis pseudoalpinus*. Although I have seen all these specimens, I had the opportunity to examine only a limited number of male genitalia. Based on the structure of these genitalia, eleven males from Misgah (Hunza) appeared to belong to *alpinus mustagatae*, seven males from Gilgit and Chitral to *cashmirensis pseudoalpinus* and one male from Darkot in the extreme north of Chitral to "normal" *P. alpinus*. This is largely in agreement with Alberti's opinion (see further below under *P. cashmirensis*).

The easternmost locality of *P. cashmirensis* known is the Safed Koh in E Afghanistan (I have seen the genitalia of the male in the BM). Wyatt & Omoto (1966) described the new subspecies *cashmirensis lilliput* from the Anjuman Valley and the Anjuman

Pass in N Afghanistan. A distributional overlap of *P. darwazicus* and *P. cashmirensis* seemed possible as *darwazicus celsimontius* was known to occur in N Afghanistan. I examined three male paratypes of *lilliput*. On dissection of two of them the genitalia appeared to belong to the *darwazicus* type and not to the *cashmirensis* type.

Geographic history of the superspecies. — Undoubtedly, the history of the superspecies is not very old, but it is (yet) impossible to date the differentiation into three species. All three appear to be confined to high altitudes. Therefore, warm periods, rather than cold, may have led to their initial isolation. But, evidently glaciations could also have brought about changes in these highly elevated mountainous areas.

8.a. *Pyrgus alpinus* Erschoff

Erschoff, 1874 — Lep. Turkestan: 24; pl. 2 fig. 18.

Type-locality: Kokand.

Distribution (Map 7). — C Asia from Serafshan throughout the mountains of W Turkestan, at least to Issyk-Kul; further, Altai and Kamschatka (Alberti, 1952a) and Vilui (Herz, 1898). Towards the south reaching Darkot (N Chitral) and Hunza (N Gilgit) (BM).

Habitat. — According to Groum-Grshimailo (1890) it is confined to the alpine meadow zone (in Pamir), from 3200—4300 m, in the Kounjout Mts. even higher; on the Col Beik at 4800—5000 m.

Biology. — Presumably monovoltine. Groum-Grshimailo (l.c.) recorded as flight period June-July, but specimens are also known from August and September.

Geographic variation. — As pointed out by Alberti (1952a) specimens from Serafshan to Kamschatka are all alike. However, east of Pamir a small form occurs in a restricted area.

Pyrgus alpinus alpinus Erschoff

Material examined. — 89 ♂ 40 ♀ : 3 ♂ Serafshan (BM, ML), 2 ♂ 1 ♀ Samarkand (BM), 2 ♂ 1 ♀ Issyk-Kul, 32 ♂ 13 ♀ Tian Shan (BM, ML, RJ), 23 ♂ 12 ♀ Naryn River (BM, ML), 17 ♂ 8 ♀ Ferghana (BM, RJ), 1 ♂ 1 ♀ Alai (ML), 3 ♂ 2 ♀ Kashgar (BM), 1 ♂ Darkot (Chitral) (BM). Apart from these specimens I found a number of specimens in the BM collections of which Evans, evidently, did not trust the labels: 3 ♂ 1 ♀ "Amoor" (Crowley Bequest), 1 ♂ "Amur", 1 ♂ "Russia", 1 ♀ "Siberia".

Distribution. — The whole range of the species except that of ssp. *mustagatae*.

Subspecific characters. — For differences with ssp. *mustagatae*, see under that subspecies.

From the other species of the superspecies (except *cashmirensis pseudoalpinus*) the present species is easily distinguished by the strongly spotted upper side and particularly, by the two obvious white spots at the tornus uph.

Pyrgus alpinus mustagatae Alberti

Alberti, 1952 — Zeitschr. Lepid. 2: 80.

Type-locality: Mustagh Ata, Yarkand.

Material examined. — 11 ♂ Hunza (Misgah) (BM).

Distribution. — Presently only known from the type locality and from N Gilgit (material examined).

Subspecific characters. — Small, 11.2—12.2 mm. Above as ssp. *alpinus*. Unh spots reduced, central spot not projecting towards the base of the wing.

Note. — Alberti (l.c.) considered it a high altitude race but did not record exact altitudes of material examined. As ssp. *alpinus* also seems to be confined to high altitudes (see above, the habitat of the species), it is not very significant to call ssp. *mustagatae* a high altitude form.

Geographic history. — The absence of geographic variation over such a wide range may indicate a fast and recent expansion of the range, not earlier than Last Glacial and even now, the range may be more continuous than the present data suggest. Presumably *P. alpinus* spread from C Asia, as all related forms and species occur there. Besides, if *alpinus* originally was an East Siberian species one would have expected its occurrence in N America, for this highly cold-adapted species must have been able to cross Beringia.

8.b. *Pyrgus cashmirensis* Moore

Moore, 1874 — Proc. Zool. Soc. Lond. 1874: 274; pl. 42 fig. 7.

Type-locality: Kashmir.

Distribution (Map 7). — From Safed Koh and Chitral through Kashmir to Kumaon; Bhutan (BM). The known localities suggest that the species may also occur in Nepal.

Habitat. — In Gilgit at least to 4300 m (BM).

Biology. — Unknown.

Geographic variation. — Although the male genitalia do not seem to vary geographically, there is a remarkable variation in external characters leading to the recognition of two subspecies: in Chitral and Gilgit a form occurs which is externally indistinguishable from *P. alpinus*. This was discovered by Alberti (1952) who had two males available. As mentioned earlier, I examined male genitalia of only few specimens. As I am not entirely certain about other specimens from Chitral and Gilgit, only the specimens thus examined by me will be enumerated below. It is, however, interesting to note that 55 ♂ and 25 ♀ from Chitral, Gilgit, etc. in the BM vary in external characters from nearly *P. cashmirensis* to completely *P. alpinus*.

Pyrgus cashmirensis cashmirensis Moore

Material examined. — 76 ♂ 28 ♀ : 1 ♂ Safed Koh (BM), 4 ♂ 4 ♀ Baltistan (BM), 141 ♂ 17 ♀ Kashmir (BM, RJ), 12 ♂ 2 ♀ Ladakh, 5 ♂ 1 ♀ Lahoul, 10 ♂ 3 ♀ Kulu, 1 ♂ Kumaon, 2 ♂ Bhutan (all BM).

Distribution. — The range of the species except Chitral and Gilgit.

Subspecific characters. — Easily distinguished from ssp. *pseudoalpinus* (and from *P. alpinus*) by the reduced spots, above; spots upf small, uph faint or absent.

Pyrgus cashmirensis pseudoalpinus Alberti

Alberti, 1952 — Zeitschr. Lepid. 2: 85.

Type-locality: Gilgit.

Material examined. — 6 ♂ Chitral, 1 ♂ Gilgit (BM).

Distribution. — Confined to Chitral and Gilgit. Shirôzu & Saigusa (1963) recorded this form from W Pakistan under the name *Pyrgus alpinus alpinus*. They gave nice figures of male genitalia (fig. 2) and the upper- and underside of two males (not one male and female, as stated). The localities in W Pakistan are: Mochodan-Tikatoki and Tikatoki-Diwan Gal.

Subspecific characters. — Externally like *P. alpinus*.

Variation. — The male examined from Gilgit had a transitional facies and resembled more ssp. *cashmirensis* than *P. alpinus*. There may be a continuous variation from the *cashmirensis* facies to the *alpinus* facies.

Geographic history. — Presently, nothing can be said on this subject.

8.c. *Pyrgus darwazicus* Groum-Grshimailo

Groum-Grshimailo, 1890 — in Romanoff, Mém. Lép. 4: 501; pl. 21 fig. 5.

Type-locality: Darwaz (Touptschek).

Distribution (Map 7). — In collections, a very rare species of which only few localities are known. In the BM there are specimens from Darwaz, Samarkand and Trans-Alai. According to Alberti (1952a) further only known from the Alai, the Sebak Valley and the Nuksan Pass (NE Hindu-Kush). From these scanty data Alberti thinks that *P. alpinus* and *P. darwazicus* are possibly partly sympatric (*P. alpinus* is also known from Samarkand and Alai). However, by the locality "Samarkand" usually the province is meant and not the city (the same applies to Bokhara). The province has a length of more than 500 km and a mountainous part stretching over more than 400 km. Likewise, the Alai is an extensive region. Therefore, on the ground of the few specimens known there is no reason to consider the two species sympatric in these regions.

As stated above, the race described by Wyatt & Omoto (1966) as *Pyrgus cashmirensis lilliput* appeared to be a race of *P. darwazicus*. The known localities of *P. darwazicus* can thus be supplemented by Bala Quran and the Anjuman Pass, both in the Anjuman Valley in the Hindu-Kush, southwest of the Sebak Valley.

Besides, Wyatt & Omoto recorded possible *P. darwazicus* specimens from the Anjuman Pass (1 ♂) and from the Shiva Mts. (NE Badakhshan) (1 ♂, 2 ♀). I examined one of the females of the Shiva Mts. This rather worn female is geographically as well as externally intermediate between ssp. *darwazicus* and ssp. *celsimontius*, perhaps somewhat closer to ssp. *celsimontius*. I also examined the genitalia, but assurance on the identification cannot be given, as the female genitalia of a true *P. darwazicus* are unknown to me. For the present time it seems best to classify the Shiva female as *P. darwazicus* (it will be enumerated below under ssp. *celsimontius*).

Habitat. — All known specimens are from higher altitudes (as far as recorded): 2800—4100 m, the alpine meadow zone (Groum-Grshimailo, l.c.; Alberti, l.c.; Wyatt & Omoto, l.c.).

Biology. — Unknown.

Geographic variation. — There is a marked variation in size, in the extension of the spots and sometimes some variation in the shape of the antistyle, but the material is too scarce to be certain.

***Pyrgus darwazicus darwazicus* Groum-Grshimailo**

Material examined. — 3 ♂ 2 ♀: 2 ♂ Darwaz, 1 ♂ 1 ♀ Samarkand, 1 ♀ Trans-Alai (all BM).

Distribution. — Southern C Asia, north of Afghanistan.

Subspecific characters. — Dark, with reduced spots; upf spots very small, uph spots very faint or absent, unh spots reduced and with vague outline, recalling *Pyrgus cacaliae*.

***Pyrgus darwazicus celsimontius* Kauffmann**

Kauffmann, 1952 — in Alberti, Zeitschr. Lepid. 2: 85—86; figs. 3, 4.

Type-locality: Sebak Valley (Badakhshan).

Material examined. — 1 ♀ Shiva Mts. (CW).

Distribution. — Probably a limited distribution in Badakhshan.

Subspecific characters. — Strongly spotted, somewhat like *P. alpinus*. Uph with very obvious central spots, but remainder of median band almost absent, submarginal spots indicated by greyish scales. Smaller than ssp. *darwazicus*, according to the original description ♂ 24—26 mm, ♀ 29 mm, undoubtedly "from tip to tip".

Variation. — The female examined has less distinct spots than the figure of ssp. *celsimontius* in the original description. It may be transitional to ssp. *darwazicus*; see also above. Wing-span from tip to tip: 27.5 mm, length of fore wing 14.1 mm.

***Pyrgus darwazicus lilliput* Wyatt & Omoto**

Pl. 1 Fig. 18, 36

Wyatt & Omoto, 1966 — Entomops 1966 (6): 195—196.

Type-locality: Bala Quran (Anjuman Valley, Hindu-Kush).

Material examined. — 3 ♂ Anjuman Valley (paratypes) (CW).

Distribution. — Only known from the Anjuman Valley.

Subspecific characters. — Very small, ♂ 10.5 mm; according to the original description the males are 10—12 mm, the female 13 mm. Above, better marked than in ssp. *darwazicus*, more or less like *P. cashmirensis*; uph submarginal median spots clearly visible, according to the original description in the female very distinct. Underside, dark, recalling ssp. *darwazicus*.

In the male genitalia the antistyle seems to be less pointed. However, no data on individual variation can be presented, as genitalia of only two males were examined. Likewise, the individual variation in the nominate subspecies is unknown (cf. Alberti, 1952a).

Geographic history. — At present no information can be given on this subject.

9. *Pyrgus andromedae* Wallengren

Wallengren, 1853 — Of. K. Vet. Akad. Förh. 10: 25.

Type-locality: Dalarne (selection by Opheim, 1953).

Distribution (Map 8). — Arcto-alpine and confined to Europe. In Scandinavia confined to the mountains from the North Cape south to Dovre and Dalarne, most localities being situated within the Arctic Circle (for detailed distribution map, see Nordström, Opheim & Valle, 1955).

Widely distributed in the Pyrenees, from Col du Pourtalet in the Basses Pyrénées

(RJ) to Mont Canigou in the Pyrénées Orientales (Dufay, 1961); from the Spanish side only recorded from Ordesa, Santuario de Nuestra Señora de Las Bordas (Valle de Arán) (Rondou, 1932; Manley & Allcard, 1970). In the Alps it is one of the most universally distributed species of the genus and almost anywhere above 1700 m one may expect to find it (Warren, 1926). Known from the Basses Alpes and Alpes Maritimes to S Bayern, Styria and the Triglav (NW Yugoslavia) (a.o. Alberti, 1927; Verity, 1940, 1947; Kauffmann, 1951; see also under "Material examined").

Further only known from the high mountains of Yugoslavia: Treskavica, Prenj, Velez and Baba planina near Gacko, all in Bosnia (Rebel, 1904); Bretherton (1966) records the species from the Shar planina, between Serbia and Macedonia.

Habitat. — Mountain slopes, moorland, usually near water. According to Warren (1926), banks of a mountain torrent are a favorite haunt, though swampy ground of any kind is equally suited. In the Alps usually from 1600 to 2500 m (Kauffmann, 1951), but single specimens may be found up to 3300 m (Warren, 1926, Verity, 1940). Unlike *P. cacaliae* it is rarely abundant (Warren, l.c.). In Scandinavia in the upper birch zone and beyond the tree limit (Nordström, e.a., 1955; Gullander, 1959).

Biology. — Monovoltine; flight period between the end of May and half August, depending on altitude (Kauffmann, l.c.). Larval stages and food plants unknown.

Geographic variation. — In spite of the great disjunction in the distributional area, geographic variation is unknown for this species. Even a fervent splitter like Kauffmann (1951) failed to find geographic variation.

Material examined. — 121 ♂ 56 ♀: 19 ♂ 21 ♀ N Scandinavia (Norway, Sweden, Finland) (BM, ML, RJ), 3 ♂ 1 ♀ Pyrenees (Basses Pyr., Col du Pourtalet; Hautes Pyr.) (BM, RJ), 7 ♂ 2 ♀ French Alps (Basses Alpes, Hautes Alpes, Savoie) (BM), 47 ♂ 16 ♀ Switzerland (BM, ML, ZMA), 5 ♂ 2 ♀ Bavaria (Oberstdorf, Allgau, Garmisch) (BM, ML, RJ), 2 ♂ Italia (Aosta) (BM), 36 ♂ 13 ♀ Tirol and Austria (BM, ML, RJ), 2 ♂ Bosnia (Trenj) (BM), 1 ♀ Hungary ("Hungrie") (BM).

Geographic history. — The postglacial history of this species must have run almost parallel to that of *P. cacaliae*. Apart from coincidences, the difference in the distributional areas may be due to a slight difference in habitat preference. There are no traces of a disjunction during the Last Glaciation. See also Chapter 2.d.

10. *Pyrgus cacaliae* Rambur

Rambur, 1839 — Faune entom. de l'Andalousie 2: pl. 8 figs. 6, 7, k.

Type-locality: Grande-Chartreuse de l'Isère (Verity, 1925).

Distribution (Map 9). — Pyrenees, Alps, southern Carpathians, Balkan Mts. and Rila Dag. In the Pyrenees only few localities are known, situated in Andorra, and in the départements Pyrénées Orientales, Ariège and Hautes Pyrénées (Caradja, 1893; Rondou, 1932; Picard, 1946, 1947). In the Alps widespread, from the Alpes Maritimes to the Schneeberg in Lower Austria (see Material examined). In the southern Carpathians only known from the Bucegi Mts and from Kronstadt (Niculesci, 1968 in litt.; Higgins & Riley, 1970; BM). In Bulgaria known from the Central Balkan Mts (Drenowsky, 1909, 1910) and the Rila Dag (Züllich, 1936—37; BM).

Habitat. — Moist and dry, flowery localities at high altitudes. In the Pyrenees not below 2000 m (Picard, 1947), in the Alps usually from 2000 m to 2600 m, rarely from

1500 m upward (Verity, 1940; RJ), in the Balkan Mts. not below 1800 m (Drenowsky, 1910). In the Alps much more local than *P. andromedae*, but often very abundant (Warren, 1926; Verity, 1940).

Biology. — Monovoltine, from the last part of June to half August; the flight period in the Alps lasts about five weeks (Kauffmann, 1951).

Thanks to a partly succeeded breeding experiment of Kauffmann (1954c) we know that the larvae hibernate at a very young stage: a few days after hatching they enter diapause, in the soil or between leaves, spun together; for food plants *Potentilla aurea* and *Sibbaldia procumbens* (both Rosaceae) are considered; the often mentioned *Tussilago farfara* (Compositae) (e.g. Verity, 1940; Higgins & Riley, 1970) is probably not accepted as food plant by the larvae.

Geographic variation. — A species restricted to high altitude is apt to produce morphologically distinguishable, local forms. The present species, however, shows little variation, individual or geographic. The variation mainly concerns the extension of the markings. In the same locality specimens without spots above (forma *caecus* Reverdin, 1912) occur together with rather well-marked specimens.

According to Picard (1947), eleven out of twelve specimens studied from the Pyrenees differed from specimens from the Alps in a greatly enlarged basal spot in space 7 unh. On this ground he described a new subspecies *pyrenaens*. I have seen no material from the Pyrenees, but it is, of course possible that the enlarged basal spot is a constant characteristic of the Pyrenean populations and it may be useful to distinguish the subspecies *pyrenaens*. But as the difference is small and the material scanty and as, for the present study, the distinction of subspecies is only a means, not an aim, mentioning of Picard's description may suffice.

Kauffmann (1951) described the subspecies *prosensis* from St. Gotthard-Hospiz and neighbouring localities. This form differs from the typical form in being larger, 14.2—15.1 mm against 13.7—14.9 mm, with larger spots above, unf whitish and unh yellowish with still more indistinct markings. Kauffmann (p. 342) says that "this subspecies forms about two-thirds of the population". This is, of course, a careless way of saying that about two-thirds of the specimens of the subspecies have the above-mentioned characteristics. Apparently, it is an extreme variation. However, the combination of a large size, large spots and yellowish unh seems to be more characteristic than the occurrence of all these characters apart, as all can be found elsewhere, particularly the yellowish unh. The large spots may be the most characteristic, but as there is so much overlap in all three characters mentioned above, I doubt whether it is useful to recognize *prosensis* as a separate subspecies.

According to Higgins & Riley (1970) the white spots upf are larger in the specimens from the Carpathians than in specimens from the Alps. I saw only 1 ♂ and 1 ♀ from Kronstadt. Like the Bulgarian specimens these did not differ remarkably from specimens from the Alps.

Material examined. — 173 ♂ 121 ♀: 5 ♂ 3 ♀ Alpes Maritimes (BM), 34 ♂ 11 ♀ Basses Alpes (BM, RJ), 62 ♂ 53 ♀ Swiss Alps (BM, ML, ZMA, RJ, HC), 4 ♀ Bavaria (Allgäu; "Germania") (ML, BM), 56 ♂ 39 ♀ Tyrol (from Ortler to Gross Glockner) (BM, ML, ZMA, RJ, HO), 9 ♂ 8 ♀ Carinthia (BM, RJ), 1 ♂ Radstädter Tauern (RJ), 2 ♂ Steiermark (Hochschwab) (ML, RJ), 2 ♂ 1 ♀ Lower Austria (Schneeberg) (ML, RJ), 1 ♂ 1 ♀ Rumania (Kronstadt) (BM), 3 ♂ 3 ♀ Bulgaria (Rila Dagh, Musalla Mts) (BM).

Geographic history. — The present localities of *P. cacaliae* must be considered post-glacial refugia for this cold-adapted species. During the Last Glacial the species apparently, had a continuous distribution area, somewhere between the land ice in the north and the glaciers of the Alps. At any rate, there are no traces of an earlier than a postglacial disjunction. For a reconstruction of the more ancient history of the species, see Chapter 2.d.

11. *Pyrgus centaureae* Rambur

Rambur, 1839 — Faune entom. de l'Andalousie 2: pl. 8 fig. 10.

Type-locality: Dalécarlie (= Dalarne).

Distribution (Map 9). — Discontinuously Holarctic: Scandinavia, Siberia, North America. In Scandinavia widely distributed, from S Norway and C Sweden to the Barents Sea and throughout Finland (for details, see Nordström, Opheim & Valle, 1955). East of Finland the species is only known from the formerly Finnish districts (Kaisila, 1947). Undoubtedly the species occurs further east, but records are totally absent.

The distribution in Siberia is very imperfectly known: lower course of the Yenisey, between 68° and 69° N Lat. (Trybom, 1877), Altai and Sajon Mts (a.o. Elwes, 1899; see also below, Material examined), and Vitim (Herz, 1898; BM). It is rather improbable that the species is absent from the intermediate regions.

In America widely, but possibly discontinuously distributed, from NW Yukon (NW Canada) through British Columbia southward to the high mountains of Colorado and through the NW Territories and Manitoba eastward to Newfoundland and Labrador and from there southward to N Carolina. For details, see Klots (1951), Evans (1953) and Freeman (1958).

Habitat. — A typical bog species, in the mountains up to just above the timber line (Petersen, 1954; Nordström e.a., 1955; Gullander, 1959). In Canada and Colorado as in Europe, but from New York to N Carolina (ssp. *wyandot*) on open, grassy hillsides (Klots, 1951).

Biology. — Monovoltine; flight period June-July. Larval food plant *Rubus chamaemorus* (Rosaceae) (Nordström, Wahlgren & Tullgren, 1941; Gullander, 1959).

Geographic variation. — Although America falls outside the limits of the region set for this study, the geographic variation in this part of the range may throw light on the history of the species and for this reason we should also deal with the American forms. Moreover, I will stress the subjectivity of considering the Eurasian and American forms conspecific. There is no proof of their conspecificity and we cannot *state* that they are or are not conspecific, only that we *consider* them as such.

The variation affects design, male and female genitalia. Three subspecies groups can be distinguished:

- (1) European — subspecies *centaureae* and *schoyeni*
- (2) Siberian — subspecies *sibiricus*
- (3) American — subspecies *freija*, *loki* and *wyandot*.

(1) European subspecies group. — Above with well-developed spots; unh, submarginal spots usually detached from the termen, except the spot in spaces 4—5, sometimes also the spot in space 1-c attached to the termen. Male genitalia: cuiller bluntly rounded at apex, without any specialized terminal structure; antistyle sharply turned

upwards at its ventral end. Female genitalia: sternum of eighth abdominal segment usually less sclerotized and lines of corrugation less developed than in other subspecies groups, but there exists much variation (Fig. 25, 26; see also Opheim, 1959).

Pyrgus centaureae centaureae Rambur

Material examined. — 116 ♂ 76 ♀: 12 ♂ 5 ♀ Norway (Langfjordvand, Finmark, "Norway") (BM, ML), 1 ♀ Dalarne (RJ), 93 ♂ 58 ♀ Swedish Lapland to Torne Lappmark) (BM, ML, ZMA, RJ), 2 ♂ 4 ♀ Finland (Enotekio, Lamm, "Finland") (BM, RJ), 9 ♂ 9 ♀ "Scandinavia" (BM).

Distribution. — The European part of the distributional area of the species except the localities of ssp. *schoyeni* (see below).

Subspecific characters. — See above. Differs from ssp. *schoyeni* by the heavier white markings unh; particularly the submarginal spots better developed.

Variation. — Rarely specimens occur with a basal spot in space 2 upf. Opheim (1959), who named this form *tripuncta*, knew only of eight such specimens; I have seen ten others. This variation is interesting as the basal spot in space 2 upf occurs in all American and in all Chinese *Pyrgus* species and also in *P. badachschanus* and *P. andromedae*.

Pyrgus centaureae schoyeni Opheim

Opheim, 1959 — Astarte 18: 4, fig. 1.

Type-locality: SE Norway.

Material examined. — None.

Distribution. — Isolated lowland moors in the extreme southeast of Norway (Skarnes-Saeterstoa in Sor-Odal and Bjorkelangen in Nordre Holand) (see Opheim, 1959).

Subspecific characters. — Unh ground colour very dark, spots somewhat reduced, particularly the submarginal spots and the outer spot in space 7.

(2) Siberian subspecies group. — Above spots reduced, though in some females strongly developed. The upperside varies from a sharply marked to a rather washed-out appearance, somewhat recalling *P. cacialiae*. Unh varies from sharply marked as in ssp. *centaureae* to rather vaguely marked (but with markings much sharper than in *P. cacialiae*). The submarginal spots unh in spaces 1-c and 4—5 usually extending to the termen. Male genitalia: cuiller variable, from narrow throughout and pointed at apex, to broadening and bluntly rounded at apex, with very fine spines at or near apex; anti-style as in ssp. *centaureae*. Female genitalia: sclerotization and corrugation of the sternum of the eighth abdominal segment heavier than in ssp. *centaureae*; in addition strong corrugations in the intersegmental membrane between the seventh and eighth segments (Warren, 1957).

Pyrgus centaureae sibiricus Reverdin

Reverdin, 1911 — Bull. Soc. Léop. Genève 2: 78—80, pl. 11 fig. 13, 14, pl. 13 fig. 6.

Type-locality: Altai.

Material examined. — 14 ♂ 14 ♀: 10 ♂ 11 ♀ Altai (Ongodai, Bashkaus, Tchuja Mts, Arazan), 4 ♂ 2 ♀ Sajan Mts. (Sajan, E. Sajan), 1 ♀ Vitim (all BM).

Distribution. — The Siberian part of the range of the species, but it is unknown

whether the specimens of Trybom (1877) from the lower Yenisey belong to this subspecies or rather to the Scandinavian form.

Subspecific characters. — See above.

Note. — I cannot refrain from recording a case, in which measuring by two standards makes systematics unacceptable. Warren (1926: 41—42) described the new species *chapmani*, based on four males and one female from Munko Sardyk (Sajan Mts), Vitim and "S Siberia", and added (p. 41): "This species is very close to *H. sibirica*, and though abundantly distinct anatomically, I am not able to separate the two by their superficial facies" and (p. 42): "We must rest content for the present only to record the fact that these two species exist, and hope that the future will bring us fresh light on the subject." At that time, systematics were based on the typological species concept and any morphological difference was considered proof of specific distinction. The future brought fresh light on the subject: Warren (1957) had examined one female of *sibiricus* and one female of *chapmani* and as the genitalia of these specimens were similar, he concluded (p. 376): "The slight differences in the male genitalia must be individual variations, the few specimens dissected being insufficient to demonstrate this." I fail to see why four males are insufficient to demonstrate individual variation and why two females are sufficient to demonstrate constancy. Besides, in 1926 Warren was not able to separate the females of *sibiricus* and *chapmani*, but in 1957 forgot to mention how he could distinguish the females then. Perhaps he only examined two specimens of *sibiricus* (or of *chapmani*).

I was not able to study female genitalia of *sibiricus*, but fortunately, could examine those of 12 males, in which I found a large range of variation, from the narrow and pointed *chapmani* type of cuiller, through the *sibirica* type, to almost the *centaureae* type (Fig. 55, 56). Therefore I think Warren was correct in considering *chapmani* and *sibiricus* conspecific, not because their females are alike, but rather, because there is no reason to consider them distinct, as in every species one can expect some individual variation in any character.

Moreover, if one accepts the biological species concept, one can only consider *sibiricus* a subspecies of *centaureae*. This was done by Evans (1949), who listed *chapmani* as a synonym of *sibiricus*, and *sibiricus* as a subspecies of *centaureae*. Unfortunately, Warren (1957) neglected both Evans's action and the biological species concept.

(3) American subspecies group. — Upf bar at end of cell usually better defined than in the Eurasian forms; unh submarginal spots separated from the termen throughout (except along the veins). According to Evans (1949) the basal cell spot unh is more or less widely separated from the spot near base of space 7, whereas in ssp. *centaureae* they usually adjoin. There is, however, too much variation in both ssp. *centaureae* and the American forms, to use this as a distinguishing character.

Male genitalia: cuiller somewhat variable, apex usually pointed, dorsal edge of cuiller finely spined, sometimes only a little serrated; antistyle spined or indented, but not with a sharply upturned point as in ssp. *centaureae*. Female genitalia: corrugation of the sternum of the eighth abdominal segment rather stronger and the proximal lines running straighter than usually in ssp. *centaureae*, more recalling the structure of ssp. *sibiricus*, but without the corrugation of the intersegmental membrane. (I did not examine female genitalia of American specimens, but refer to the figures and description by Warren, 1957).

Pyrgus centaureae freija Warren

Warren, 1924 — Trans. ent. Soc. Lond. 72: 56—57, pl. B, fig. 1—7.

Type-locality: Labrador.

Material examined. — 19 ♂ 5 ♀ Labrador (BM, ML).

Distribution. — Northeastern part of the American range of the species; Labrador, south to Gaspé. Western limit of this subspecies unknown (cf. Klots, 1951; Evans, 1953).

Subspecific characters. — Unh white areas well-developed, giving the hind wing a much whiter appearance than in the other American forms. Small, ♂ 13.0—13.8 mm. According to Klots (1951), the style in the genitalia of males from Manitoba to Labrador is shorter than in ssp. *wyandot*. I only examined the genitalia of nine American males (*wyandot* 2, *loki* 3, *freija* 4), but found the longest style in Labrador specimens.

Note. — The history of *freija* in literature is full of misconceptions. It is not necessary to go deeply into the subject, but it may be useful to summarize the difficulties briefly.

The form was described as a distinct species occurring in Lapland and America. Bell had called attention to *freija* as an American species in 1926; already two years later Lindsey (1928) questioned the specific rank of *freija*, comparing specimens from New Jersey, Labrador and Lapland. Therefore, Warren (1957) is incorrect, saying that: "those workers who stated that *freija* and *centaureae* were the same species were only comparing two races of *freija*; the latter and *wyandot*" (p. 375).

Another problem, viz. the occurrence of *freija* in Lapland, was dealt with extensively by Opheim (1951, 1953, 1959). Only two females from Lapland were known, attributed by Warren (1951, 1957) to *freija*, but Opheim showed that they fall within the variation of Scandinavian *centaureae*.

Pyrgus centaureae loki Evans

Evans, 1953 — Cat. Amer. Hesp.: 214.

Type-locality: Long Peak Trail (Colorado).

Material examined. — 27 ♂ 10 ♀: 5 ♂ 2 ♀ Canadian Rockies (BM, RJ), 22 ♂ 8 ♀ Colorado (South Park, Glen Cove, Bullino, Hall Valley) (BM).

Distribution. — The western part of the American range of the species; eastern limit unknown.

Subspecific characters. — Above more strongly marked than ssp. *freija*; unh white spots reduced, ground colour somewhat yellower. Larger than ssp. *freija*, ♂ 13.8—14.8 mm. The unh appears somewhat intermediate between ssp. *freija* and ssp. *wyandot*, but still closer to ssp. *freija*.

Pyrgus centaureae wyandot Edwards

Edwards, 1863 — Proc. Ent. Soc. Philadelphia 2: 21, pl. 5.

Type-locality: Long Island.

Material examined. — 11 ♂, 7 ♀: 1 ♂ New York, 8 ♂ 5 ♀ New Jersey, 1 ♂ 1 ♀ N Carolina, 1 ♂ 1 ♀ Virginia.

Distribution. — New York south to N Carolina (Klots, 1951; Evans 1953).

Subspecific characters. — Size as in ssp. *freija*. Unh spots reduced, particularly the submarginal spots, somewhat recalling the unh of *P. malvae* but spots larger; ground colour yellowish brown.

Geographic history. — For the reconstruction of the geographic history of the species the occurrence and differentiation in America is elucidating. *P. centaureae* is undoubtedly a Pleistocene invader in America, as all close relatives are cold-adapted, Palearctic species (see also Chapter 2.d). The change of habitat (undoubtedly connected with a change of food plant) in ssp. *wyandot* appears to be of a recent age.

The Bering Strait area could only be crossed by land during glacial and perhaps in early interglacial times (Petersen, 1954). If *P. centaureae* would have reached America during the Last Glacial, the ice shield which isolated ice-free Alaska from the rest of ice-free America (cf. Petersen, l.c., fig. 2), would have prevented a further expansion of the range in N America until postglacial times. The occurrence of *P. centaureae* in the high mountains of Colorado is only understandable, if we suppose that this species was present in N America before the Last Glacial. It seems that an invasion into America earlier than during the Third Glacial (i.e. during the Second Glacial or earlier) would have left behind much more differentiated forms, as the American populations would have been isolated from the Palearctic ones during the very long Second Interglacial. Consequently we may assume, that *P. centaureae* invaded America during the Third Glacial. Thus the species came into being in the Palearctic not later than during the Third Glacial.

The differentiation of the species in the Palearctic does not give a reason for supposing an earlier origin. The differentiation into a European and a Siberian group may even be of a postglacial age, but it is impossible to date the differentiation more exactly as long as the occurrence in N Russia and Siberia is so imperfectly known. Isolation during the Last Glacial could have been caused by the inundated W Siberian lowlands (cf. Moreau, 1955).

In Europe *P. centaureae* is a postglacial invader which spread to the west with the taiga to which its habitat (mire) is so closely connected. The absence of the food plant (*Rubus chamaemorus*) from the C European mountains may have caused the absence of *P. centaureae* there.

According to Petersen (l.c.) the mire species are adapted to a cold, continental climate. This can be demonstrated by the distribution of *P. centaureae* in Norway, where it is absent from the coastal regions. It is hardly probable that the species has been isolated on the western coast of Norway during the Last Glacial, as supposed by Opheim (1951), to explain the variability of *P. centaureae* in Scandinavia. At least, the optimal habitat of this species was not present during the Last Glacial along the Norwegian coast.

The origin of ssp. *schoyeni* is of a very recent, no doubt postglacial age. The fact that it is less variable than ssp. *centaureae* (Opheim, 1959) can be due to the restricted range of the former subspecies and to a restricted number of ancestor specimens.

12. Superspecies *Pyrgus malvae* Linnaeus

Taxonomy. — The taxonomy of the superspecies has been discussed in Chapter 2.b and is summarized here. The superspecies consists of three semispecies: *P. malvae*, *P. malvoides* and *P. melotis*. *P. malvae* and *P. malvoides* interbreed; interbreeding of *P. malvae* and *P. melotis* is not improbable, but has not yet been established.

Distribution. — The superspecies is distributed throughout the Palearctic (with the exception of very cold or dry regions). The distribution of the semispecies is as follows:

P. malvoides — SW Europe (Portugal, Spain, S France, S and E Switzerland, W Austria, Italy).

P. melotis — south of the Caucasus and the Black Sea.

P. malvae — the remainder of the distribution area of the superspecies.

Geographic and evolutionary history. — Various authors (Picard, 1948a, 1950a; Warren, 1957; Sichel, 1962a) have attempted to outline the geographic history of superspecies *malvae*, but only Sichel has taken the far-reaching influence of the Pleistocene glaciations into account. As shown below, each of the three semispecies can be divided into two subspecies. These subspecies clearly indicate the refugial areas of the superspecies during the Last Glacial:

<i>malvoides malvoides</i>	— Spain
<i>malvoides modestior</i>	— Italy
<i>melotis melotis</i>	— Syria
<i>melotis ponticus</i>	— E Turkey
<i>malvae malvae</i>	— SW Siberia / SE Russia / SE Europe
<i>malvae kauffmanni</i>	— S Manchuria and Korea.

The following notes are added:

(a). The differentiation into ssp. *melotis* and ssp. *ponticus* is not well understood. The Taurus Mountain System may have had influence on the geographic isolation which led to the differentiation of both forms (cf. Kosswig, 1955, fig. 12). However, the occurrence of ssp. *melotis* on the Island of Milo is rather puzzling. This led Sichel (l.c.) to the assumption of a second refugium in W Anatolia. If the specimen in the British Museum labelled "Smyrna" really originates from that locality, a W Anatolian refugium, indeed, would not be impossible. This refugium, however, seems rather improbable, because (1) it does not explain that ssp. *ponticus* instead of ssp. *melotis* occurs at the southern coast of Turkey, and (2) it would mean that ssp. *melotis* is the older form. The latter suggestion is improbable, as the differentiating character of ssp. *melotis* (mainly the white unh) does not seem primitive; or else, *melotis* has to be polytopic, for which no evidence, neither in favour nor to the contrary, exists.

There is a much more trivial explanation for the occurrence of ssp. *melotis* on the Island of Milo (? and W Turkey), viz. it may have been brought there by man as there has been lively shipping between Syria and the Aegean region since the Phoenicians.

(b). With the available data it is difficult to explain the large transitional zone between ssp. *malvae* and ssp. *kauffmanni* (Transbaicalia, Amur region), but there is no reason to regard it differently than as a zone of postglacial secondary intergradation.

Apparently the differentiation which eventually led to the origin of the three semispecies, took place in the Third Glacial. From the present distributional areas of the semispecies we may conclude that *P. malvoides* originated in a West Mediterranean refugium, *P. melotis* in an East Mediterranean refugium and *P. malvae* in an Asiatic refugium.

Sichel (l.c.) observed that *P. malvoides* does not occur in NW Africa, on the Balearic Islands and on Sardinia (and according to him, neither on Corsica). He concluded that the semispecies arose rather late, but he did not give an exact period. Evidently, he meant that the presence of *P. malvoides* in SW Europe of a rather recent time, but as *P. melotis* is absent on Crete and Cyprus and *P. malvae* in Sakhalien and Japan, this reasoning leads to the idea that the presence of superspecies *malvae* in the Palaearctic is young (i.e. the superspecies originated in a recent time or it originated elsewhere and

colonized the Palaearctic in a recent time) or that superspecies *malvae* up to a rather recent time only occurred in the interior of the Palaearctic. The only morphologic character pleading for an origin outside the Palaearctic is the bipartite uncus, a unique character among the Palaearctic *Pyrgus* species, but a normal feature in the American ones. Without other points of evidence I will leave a possible Nearctic origin of superspecies *malvae* out of consideration (see also below). Furthermore, if there is any truth in the assumption that *P. malvoides* and *P. melotis* originated in Mediterranean refugia, during the Third Glacial, their precursor must have lived in the Mediterranean during the Second Interglacial and the origin of superspecies *malvae* must date back at least as far as the Second Glacial. As the difference between *P. malvae* and *P. melotis* is less than between *P. malvoides* and the other semispecies (particularly in the lateral apophyses), it is not improbable that the differentiation into a *malvoides* ancestor and a *malvae-melotis* ancestor took place in the Second Glacial and thus the origin of superspecies *malvae* must date from an earlier period.

So the absence of superspecies *malvae* from NW Africa and many islands cannot be attributed to a recent origin of the semispecies or of the superspecies and the cause of the absence must be looked for elsewhere, probably in some unknown ecological factor.

At present nothing can be added to the geographic history of superspecies *malvae*, but a few words may be said on the evolutionary history. Where there exists a distinct genital plate in the *Pyrgus* species, it is entire, except in *malvae malvae* in which it is split into two parts. Therefore, the bipartite condition in *malvae malvae* undoubtedly has been derived from an undivided plate as found in the semispecies *malvoides* and *melotis* and in *malvae kauffmanni*.

A comparable situation exists in the male genitalia. The long processes of the lateral apophyses found in *P. melotis* and *P. malvae* probably evolved from a simpler type such as found in *P. malvoides*. There is a gradual evolution in these processes, from the slender and smooth type of *P. melotis* through the rather slender and spined type of *malvae kauffmanni* to the coarse and heavily spined type of *malvae malvae*.

The same tendency is found in the style-stylifer-antistyle: a shortening and widening from *P. melotis* (and *P. malvoides*) through *malvae kauffmanni* to *malvae malvae*.

Thus very probably, semispecies *malvae* is the most recent among the semispecies of superspecies *malvae*. Of course, this does not mean that every character of semispecies *malvae* is of recent origin, but it is very unlikely that a primitive character persisted only in this semispecies. In this light the bipartite uncus of semispecies *malvae* seems a recent character, independently originated from the bipartite uncus found in American *Pyrgus* species; this disposes of the only argument in favour of an American origin of the superspecies *malvae*.

Warren (1957) considered the bipartition of the uncus a very old character, as he found it also in *Zerynthia*, a genus of the Papilionidae which is supposed to be primitive. However, comparison of the uncus of an arbitrary species of the Hesperidae with that of any species of the Papilionidae does not seem appropriate, as these families since long are considered very distantly related (cf. Kiriakoff, 1960). Warren is undoubtedly correct in stating that the type of the genitalia found in ssp. *kauffmanni* (named *coreanus* by Warren) can be regarded as the primeval type of the semispecies *malvae* (given specific rank by Warren). Just as the lateral apophyses and the style-stylifer-antistyle, the uncus appears to change gradually from *P. malvoides* through *P. melotis* and *malvae*

kauffmanni to *malvae malvae*: in *P. malvoides* the uncus is usually apically incised, in *P. melotis* it is sometimes partly bifid, in *malvae kauffmanni* the two parts of the uncus lie close to each other, and in *malvae malvae* the uncus consists of two diverging parts. Strangely enough, the linking of *P. malvoides* to *P. malvae* through ssp. *kauffmanni* is regarded as improbable by Warren and he even states (1957: 373): "The formation of the apophyses, so markedly different in *malvoides*, suggests that it has originated from some entirely independent source." Thus he ignores the known hybridization between *P. malvae* and *P. malvoides*.

12.a. *Pyrgus malvae* Linnaeus

Linnaeus, 1758 — *Systema Naturae*, Ed. X: 485.

Type-locality: Åland Is.

Distribution. (Map 10). — Palaearctic. From Great Britain to Korea and from the Mediterranean to approximately 65° N Lat. (In Finland). The most widely distributed *Pyrgus* species (i.e. semispecies).

In Great Britain, throughout England and Wales, north to S Yorkshire (Warren, 1926; Ford, 1946); records from Ireland refer to misidentifications (Baynes, in litt.). Throughout W, C, E and SE Europe. In Norway only in the south, in Sweden north to approximately 64° N Lat., in Finland a little more to the north; for a detailed distribution map, see Nordström, Opheim & Valle (1955). In SW Europe replaced by *P. malvoides*, south of a line roughly running from Rochefort (W France, Charente Maritime) through C France, via Lyon, south of the Lake of Geneva, via St. Maurice (Valais) to Landquart (Grisons) and from there via Innsbruck curving to Istria (for references, see Chapter 2.b and under *P. malvoides*). In Italy it is only known from Sappada in the northeast (Verity, 1940).

Throughout the Balkans and Greece; see also under semispecies *melotis*. East of the Bosphorus the distribution is poorly known; I saw specimens from Brussa (2♂ 4♀), Zonguldak (1♂) and Amasia (1♂) (BM). From the last locality also *melotis ponticus* is known, which form occurs much further west, near Ankara (Çubuk Baraj). This makes the correctness of the label of this single *P. malvae* specimen from Amasia at least questionable. De Lattin (1950) recorded a male and a female of *P. malvae* taken at Sivrice in E Turkey and he stated: „Wie die Genitaluntersuchung ergibt, handelt es sich um echte *malvae*, nicht um *malvoides* Elw. u. Edw." (p. 326). Possibly, these specimens belong to *melotis ponticus*, which sometimes has a partly bipartite uncus and also in other respects resembles *P. malvae* much more than *P. malvoides*. However, De Lattin also recorded a male of *P. melotis* from Sivrice of which he examined the genitalia. This may indicate a variable population or a distributional overlap of ssp. *melotis* and ssp. *ponticus* (in which case they cannot be considered conspecific) or of *P. melotis* and *P. malvae*.

According to Alberti (1969), not yet found in the Caucasus (replaced there by *melotis ponticus*), but north of the Black Sea only *P. malvae* occurs and not *melotis ponticus*. In Russia widely distributed, at least as far north as Kotlas (61° N Lat.) (Krulikovskiy, 1909).

Throughout Siberia; some northern localities are Antsiferovo on the Yenisey (59° N Lat.) (Trybom, 1877) and the Vilui in NE Siberia (63°—64° N Lat.) (Herz, 1898). Southward to Pamir (Groum-Grshimailo, 1890) and Korea (Alberti, 1955; Warren, 1957).

Habitat. — Flowery places, on dry and on marshy ground; from sea-level to 2000 m in the Alps and in Macedonia (own observation) and to 3000 m in Pamir (Groum-Grshimailo, 1890). At least in Switzerland more common at low than at high altitudes (Wiltshire & De Bros, 1966).

Biology. — Monovoltine; usually flying in May and June. In southern localities it may be bivoltine, e.g. in Macedonia (Thurner, 1964); in the British Museum there is a nice series of Hungarian specimens from every month from April to October. According to Kurentsov (1949), north of Vladivostok two broods, in May and August.

P. malvae hibernates as chrysalis (Forster & Wohlfahrt, 1955; Gullander, 1959; etc.).

Various species of Rosaceae have been recorded as food plants, belonging to the genera *Comarum*, *Fragaria*, *Potentilla*, *Rubus* and *Agrimonia* (e.g. Verity, 1940; Bergmann, 1952; Forster & Wohlfahrt, 1955; Guillaumin, 1964). Some authors also mention *Coronilla* (Papilionaceae) (Verity, Bergmann) and *Dipsacus* (Dipsacaceae) (Verity) as food plants.

Geographic variation. — It is surprising that *P. malvae*, though individually highly variable, does not vary geographically from England to Lake Baikal. Only in the extreme east of the distribution range, in the Sikhote-Alin range and Korea, a form occurs which is obviously different by the genitalia and slightly by the facies. Transbaicalia and the Amur region are populated by transitional forms.

Pyrgus malvae malvae Linnaeus

Material examined. — 729 ♂ 372 ♀: 44 ♂ 29 ♀ England (BM, ZMA, RJ), 141 ♂ 55 ♀ Netherlands (ML, RJ), 36 ♂ 12 ♀ Belgium (BM, ML, ZMA, RJ), 2 ♂ Luxembourg (ZMA), 128 ♂ 68 ♀ France (south to Charente Maritime, Cantal and Savoie) (BM, ML, ZMA), 5 ♂ 2 ♀ Norway (BM), 1 ♂ Sweden (BM), 6 ♂ 4 ♀ Finland (BM, ML), 1 ♂ Denmark (BM), 65 ♂ 50 ♀ Germany (BM, ML, ZMA, RJ), 19 ♂ 6 ♀ Switzerland (Geneva, Lausanne, Vaud, St. Gallen, Luzern, Zürich) (BM, ML, RJ), 62 ♂ 38 ♀ (N Tyrol, Carinthia, Austria Inf.) (BM, ML, RJ), 2 ♂ 3 ♀ Istria (BM), 8 ♂ 12 ♀ Czechoslovakia (BM, ZMA), 46 ♂ 21 ♀ Hungary (BM, ML, ZMA), 59 ♂ 21 ♀ Yugoslavia (BM, ML, ZMA, RJ), 6 ♂ 3 ♀ Bulgaria (BM, ML), 4 ♂ Rumania (ML), 25 ♂ 8 ♀ Greece (Macedonia, Olympus, Parnassus) (BM, ML), 29 ♂ 10 ♀ Bosphorus (BM), 4 ♂ 4 ♀ W Turkey (Brussa, Zonguldak, Amasia) (BM), 17 ♂ 10 ♀ Russia (Leningrad to Novorossiisk and Uralsk) (BM), 1 ♂ 1 ♀ W Siberia (Turgai, Kansk) (BM) 7 ♂ 2 ♀ Altai (BM), 1 ♂ E Sajan (BM), 2 ♂ Irkutsk (BM), 10 ♂ 3 ♀ Turkestan (Alexander Mts to Alai) (BM, ML).

Distribution. — The range of semispecies *malvae*, eastward to Lake Baikal.

Subspecific characters. — Differs from ssp. *kauffmanni* in the male genitalia by the two parts of the uncus which are set obliquely to the tegumen, by the coarser and more strongly curved processes of the lateral apophyses and by the broader style-stylifer; in the female genitalia by the genital plate which is divided into two parts. The differentiation in the facies is slight, see ssp. *kauffmanni*.

Variation. — Apart from many forms of individual variation two forms have been described as subspecies:

elegantior Verity, 1934. — Large, 11–12 mm; above a less black, warmer tinge, spots smaller, particularly the submarginal spots; unh ground colour more brownish or reddish than greenish, veins outlined in yellow instead of white. According to Verity

(1947) and Kauffmann (1951) this form occurs in the west of Switzerland and in France south of the Lake Geneva. However, specimens agreeing with the above description also occur in S Germany and, particularly, in Yugoslavia, where they fly with other forms. Perhaps an ecophenotypic variation.

lucarius Kauffmann, 1951. — Large, 11.7—12.8 mm; above ground colour very black with large spots and many whitish hairs. Unf black with strongly contrasting white spots; uph ground colour ochreous-brown to chocolate-brown or dark grey, rarely reddish, veins little contrasting.

According to Kauffmann this form occurs in C Switzerland. It is, however, not at all confined to that country but it occurs as an individual variation throughout C, E and SE Europe. I have seen specimens of this form taken as far north as the Netherlands, but almost all these examples are smaller and still further north the specimens are invariably smaller than *lucarius*.

A striking individual form is *taras* Bergsträsser, 1780. In this form the spots upf are strongly enlarged and partly coherent, while the spots uph are reduced. Extremes of this variation from W. Germany have more than half of the upperside of the fore wings white, only intersected by brown veins (Pl. 4 fig. 61, 70).

Transitional zone: Transbaicalia and Amur region. According to Warren (1957) this region is populated by forms transitional between ssp. *malvae* and ssp. *kauffmanni*. I have examined the genitalia of only five males from this region. Indeed, they turned out to be somewhat intermediate, though more resembling ssp. *malvae* than ssp. *kauffmanni*. With regard to the facies I could not distinguish these and other specimens from this region from ssp. *malvae*.

Material examined. — 11 ♂ 11 ♀ : 6 ♂ 2 ♀ Chita, 3 ♂ 7 ♀ Jablonowyj Khrebet (= Apfelgebirge), 2 ♂ 2 ♀ Amur (all BM).

Pyrgus malvae kauffmanni Alberti

Alberti, 1955 — Zeitschr. Wiener Entom. Ges. 40: 43—46.

Type-locality: "Amur Radde".

Material examined. — 9 ♂ 1 ♀ : 9 ♂ Tjutju-ho (400 km N of Vladivostok), 1 ♀ Amur (all BM).

Distribution. — Presumably confined to the Ussuri region and Korea. Data on the distribution in Korea are very scarce; Alberti (l.c.) mentions Seishin (N Korea); Warren (1957) described the same form from Hakugan under the name *coreanus*.

Subspecific characters. — Male genitalia: the two parts of the uncus not diverging as those parts in ssp. *malvae*; processes of lateral apophyses more slender, less strongly curved and less strongly spined; style-stylifer more slender. Female genitalia: genital plate entire, very much like the plate found in *P. malvoides*. Unh ground colour more evenly brownish, spots often reduced. I have seen the same unh in some specimens of *melotis ponticus*.

Geographic history. — See above, under the history of superspecies *malvae*.

12.b. *Pyrgus malvoides* Elwes & Edwards

Elwes & Edwards, 1897 — Trans. Zool. Soc. Lond. 14: 160; pl. 23, figs. 27, 27-a.

Type-locality: Biarritz.

Distribution (Map 10). — SW Europe. Throughout Spain and Portugal (Manley &

Allcard, 1970). In France north to the following départements: Charente Maritime, Gironde (northern part), Dordogne, Lot, Corrèze, Cantal, Puy-de-Dôme, Loire, Rhône, Isère, Savoie, Haute Savoie (Picard, 1948a; Guillaumin, 1964). In Switzerland confined to Valais, Ticino and Grisons (Kauffmann, 1951). In Austria confined to the western part (Ötztaler Alpen; Innsbruck) (Kauffmann, 1955).

Habitat. — As that of *P. malvae*. At least in Switzerland (Valais) it is most common at 1500 m and higher, while *P. malvae* is more common at lower altitudes (Wiltshire & De Bros, 1966). In the Alps it has been collected up to 2500 m (Ticino; Verity, 1940), in the Pyrenees up to 2000 m (Gavarnie; own observation).

Biology. — Bivoltine; in Spain flying from March to September at low altitudes (Manley & Allcard, 1970), in France from the middle of May to the middle of June and from the middle of July to the middle of October, depending on altitude (Guillaumin, 1964). In the Alps (and Pyrenees?) at higher altitudes probably single-brooded (Kauffmann, 1950-a).

It hibernates in the pupal stage (Kauffmann, 1954c; etc.).

Kauffmann (1950a, 1954c) reared the larvae and recorded as food plants: *Fragaria vesca*, *Potentilla verna* and *P. erecta* (Rosaceae).

Geographic variation. — As in *P. malvae* various forms, apparently ecophenotypic variations and differing in size, spotting and colour, have been described as subspecies, while two geographically defined forms can be distinguished on the basis of the male genitalia. Sichel (1961, 1962b) was the first to recognize the variation in the genital armature. He found a nearly constant difference between specimens from Peninsular Italy and Sicily (34 males) and specimens from the remaining part of the range (9 males from Switzerland, 41 males from N Italy, 23 males from France, 12 males from Spain and 8 males from Portugal). I have examined the genitalia of 15 males from peninsular Italy, 5 males from N Italy, 20 males from Switzerland, 20 males from SE France and the Pyrenees, and 5 males from Spain. I can only support the findings of Sichel and I therefore distinguish the subspecies *malvoides* and *modestior*. These subspecies also differ to a certain extent in the ground colour unh, but there is much overlap (see below).

Pyrgus malvoides malvoides Elwes & Edwards

Material examined. — 385 ♂ 232 ♀: 16 ♂ 14 ♀ Portugal (BM), 63 ♂ 28 ♀ Spain (BM, ML, ZMA, HC, RJ), 94 ♂ 54 ♀ French Pyrenees (BM, ML, ZMA, HC, RJ), 123 ♂ 86 ♀ France (Landes, Gers, Aveyron, Puy-de-Dôme, Bouches-du-Rhône, Var, Alpes Maritimes, Basses Alpes, Hautes Alpes, Drôme, Isère, Savoie, Haute Savoie) (BM, ML, ZMA, RJ), 49 ♂ 31 ♀ Switzerland (Valais, Ticino, Grisons) (BM, ML, ZMA, RJ), 39 ♂ 16 ♀ N Italy (BM, ML, HC, HO, RJ), 1 ♂ 3 ♀ Istria (BM, HS).

Distribution. — That of the semispecies except peninsular Italy and Sicily.

Subspecific characters. — Male genitalia: distal edge of cuiller more strongly curved than in ssp. *modestior*; the continuation of this curve intersects the dorsal ridge of the harpe or passes well above it. External characters: Ground colour unh in both broods usually of a warmer and more reddish tinge than in ssp. *modestior* but in mountainous regions often ochreous or brown, sometimes greenish, particularly in the first brood.

Variation. — In Spain and France the male genitalia show little variation, but in Switzerland and N Italy traits of ssp. *modestior* are apparent in the genitalia of some males. Sichel (1962b) found the curvature of the cuiller in 14 % and the continuation

of the profile of harpe and cuiller in 7 % of the males examined from Switzerland and N Italy to be of the *modestior* type, but he does not mention whether he found both characters in the same specimens.

Of 25 males from Switzerland and N Italy examined I found two specimens which showed both characters of ssp. *modestior* and two specimens which showed one. Thus it seems advisable to list the Swiss and N Italian populations as ssp. *malvoides*. The material examined is insufficient to establish how ssp. *malvoides* and ssp. *modestior* pass into each other, but from Emilia southward *malvoides* traits in the male genitalia appear to be very rare (see ssp. *modestior*).

For forms described on the basis of differences in size, colour and extension of the white spots is referred to Verity (1940, 1947) and Kauffmann (1951). Only two forms are mentioned here:

(1) *pyrenaicus*, Tutt, 1906, has given some nomenclatural difficulties. It was described as an individual variation taken in the Pyrenees. Warren (1926) gave the Pyrenean form of *Pyrgus carthami* the same name. Verity (1928) therefore thought it necessary to replace this name by *microcarthami*, but Warren (1929: 149) pointed out clearly that "the fact that there happens to be an ab. *pyrenaica*, Tutt, of another species in the genus in no way invalidates my race *pyrenaica*". It is surprising to find the name *microcarthami* as a subspecific name for N Spanish *malvoides* in Manley & Allcard (1970).

(2) *semiconfluens* Reverdin, 1911. An individual variation comparable with the form *taras* in *P. malvae*, viz. spots upf very enlarged and more or less confluent. I have not seen such extreme specimens as mentioned under *P. malvae*.

Pyrgus malvoides modestior Verity

Verity, 1929 — Trab. Mus. Ci. Nat. Barcel. 11: 7.

Type-locality: Tuscany.

Material examined. — 53 ♂ 25 ♀ : 41 ♂ 17 ♀ Peninsular Italy (Bologna to Calabria) (BM, ZMA, HC, RJ), 12 ♂ 8 ♀ Sicily (BM).

Distribution. — Peninsular Italy and Sicily.

Subspecific characters. — Male genitalia: distal edge of cuiller less narrowly curved; the continuation of this curve coincides with the dorsal ridge of the harpe.

External characters: the specimens of the first generation as in ssp. *malvoides*, but rarely with the warm reddish tinge unh often found in ssp. *malvoides*. The specimens of the second generation usually with a paler unh than specimens of ssp. *malvoides*, but otherwise as variable as in that subspecies.

Variation. — As stated above, males with *malvoides*-like genitalia are rare in Peninsular Italy and Sicily. I saw one male taken at Pistoia (Tuscany) with the harpe-cuiller profile of the *malvoides* type and one male from Calabria with both the curvature of the cuiller and the harpe-cuiller profile of the *malvoides* type.

An interesting individual variation is the form which has been named *melotiformis* by Verity (1929): ground colour unh extremely pale, recalling *P. melotis*.

Geographic history. — Possibly the plains of the Po have retarded the postglacial extension of ssp. *modestior* towards the north. Evidently ssp. *modestior* reached N Italy and Switzerland not earlier than ssp. *malvoides*. The data available are not yet conclusive, but it can be supposed that ssp. *modestior* and ssp. *malvoides* came into a postglacial

contact in the southern Alps, forming a hybrid population which extended its range into the central Alps.

See further above, the history of superspecies *malvae*.

12.c. *Pyrgus melotis* Duponchel

Duponchel, 1832 — Lép. France; Suppl. 1: 251; pl. 42 figs. 1, 2.

Type-locality: Island of Milo.

Distribution (Map 10). — East Mediterranean. W Anatolia to the Caucasus (Alberti, 1969) and the Jordan Valley (Hemming, 1932; BM); Milo Is. The distributional limits are badly known. The westernmost localities from where I have seen specimens of this species are Çubuk Baraj (north of Ankara), Aksehir, Egerdir and Antalya. According to Alberti (1969), it is widely distributed in Transcaucasia, but apparently there are no records of its occurrence in Iraq and Iran.

Habitat. — Not recorded but presumably as that of *P. malvae*. From 250—275 m below sea level (Jordan Valley; Hemming, 1932) up to 2600 m (Caucasus; Alberti, 1969). In the Lebanon very common up to $\pm$ 1700 m (Nicholl, 1901). In Israel (and possibly elsewhere) not in the Eremian regions (Amsel, 1933).

Biology. — Bivoltine. Ssp. *melotis* may have a third brood (Graves, 1925; Hemming, 1932). According to Milyanovsky (1964) also in Abkhaziya a third brood.

Food plants unknown.

Geographic variation. — There is much confusion about the taxonomic status of the forms *ponticus* and *melotis* (see also Chapter 2.b). They are usually considered specifically distinct, evidently without any other reason than the fact that they differ with regard to the facies and the genitalia. The difficulties are partly or entirely due to the scarcity of ssp. *ponticus* in collections, e.g. in the British Museum there are only 14 ♂ and 9 ♀. I could examine rather numerous specimens with many transitional forms between ssp. *ponticus* and ssp. *melotis*. As stated above (Chapter 2.b), no constant differences were observed in the male genitalia. In both ssp. *ponticus* and *melotis* these are rather variable; in *ponticus* this variation may be partly geographic, see below. The facies is very variable in both forms; the most important, if not the only, difference, is the colour unh; in ssp. *melotis* the unh is partly to entirely white, with very faint spots, in ssp. *ponticus* the unh is usually brownish-ochreous or greenish with well-defined spots. However, intermediate forms occur, especially in N Syria and S Turkey.

Pyrgus melotis melotis Duponchel

Material examined. — 79 ♂ 26 ♀: 4 ♂ 1 ♀ "Greece" (BM), 1 ♂ "Smyrna" (BM), 1 ♀ Antakya (BM), 70 ♂ 23 ♀ Syria (BM, ML), 4 ♂ Lebanon (BM, ML, RJ), 1 ♂ 1 ♀ Jordan Valley (BM). According to Evans (1949) the specimens labelled "Greece" in the British Museum probably originate from Milo Is.

Distribution. — N Syria to the Jordan Valley. Presumably also further north: De Lattin (1950) recorded this subspecies from Gaziantep and from Sivrice, which is much further north.

Subspecific characters. — Unh white or with white streaks, spots faintly visible.

Variation. — Already Graves (1925) noted the great variation in this form with regard to the distinctness of the spots unh, the size of the spots above and the size of

the butterfly. I have seen males from N Syria measuring 10.9 to 15.0 mm! Hemming (1932) described the "subspecies" *jordana* from the Jordan Valley, characterized by its large size, large spots above and a very white unh. Evidently, Hemming did not know that these characters do occur in other areas of distribution of ssp. *melotis* as well (he only compared his *jordana* with specimens of ssp. *melotis* from Lebanon).

The unh varies from white to nearly *ponticus*-like; some specimens from N Syria are difficult to distinguish from *ponticus*.

Pyrgus melotis ponticus Reverdin

Reverdin, 1914 — Bull. Soc. Lép. Genève 3: 66—72; pl. 3 figs. 6, 12; pl. 4 figs. 2, 3.

Type-locality: Amasia (Turkey).

Material examined. — 106 ♂ 26 ♀ Turkey (Antalya, Egerdir, Aksehir, Çubuk Baraj, Amasia, Kodos, Yozgat, Gümüşhane, Seki Yaila, Boz Dag, Mersin) (BM, RJ).

Distribution. — The range of the semispecies except that of ssp. *melotis*, i.e. north of Syria.

Subspecific characters. — Unh not white or with white streaks; brownish, ochreous or greenish with well-defined spots.

Variation. — ♂ 10—14 mm. The specimens from the Boz Dag (18 ♂ 2 ♀) are rather large (12—14 mm), dark above (with very little light superscaling), spots uph reduced. Most specimens from Aksehir (75 ♂ 14 ♀) are smaller and much more extensively spotted, but some are indistinguishable from the examined specimens from the Boz Dag.

I studied the genitalia of 25 males from Aksehir and 15 males from the Boz Dag. All specimens from Aksehir appeared to possess an entire uncus while all specimens from the Boz Dag showed a partly bifid uncus. With more material available from various parts of the range of ssp. *ponticus*, a marked geographic variation may be proved to exist.

The single specimen (♂) from Mersin has a pale ground colour unh, indicating the influence of ssp. *melotis*.

Geographic history. — See above, the history of superspecies *malvae*.

13. *Pyrgus serratulae* Rambur

Rambur, 1839 — Faune entom. de l'Andalousie: pl. 8 figs. 9, m.

Type-locality: Spain.

Distribution (Map 11). — From Spain to Transbaicalia; presumably continuously distributed from France to Transbaicalia, but isolated populations, at least in Europe, occur north and south of the main range.

In Spain presumably confined to the larger mountain regions: from the Pyrenees and the Cantabrian Mountains south to the Montes Universales and Sierra de Gredos, and probably discontinuous in Sierra Nevada (Warren, 1926; Manley & Allcard, 1970; material examined).

In Italy also confined to the larger mountain regions: the Alps, Sibillini Mts., Abruzzi and Monte Meta (Verity, 1940).

Throughout France, except the northwestern part. In W Germany northward to a line approximately from Koblenz to the Harz, in E Germany through the valley of the Saale southward (Alberti, 1927; Bergmann, 1952). Further north found in Mecklenburg

and Pommern (Urbahn, 1939; Friese, 1956); two specimens have been taken in Denmark (Wolff, 1939), but were probably of foreign origin (Opheim, 1956). Throughout C, E and SE Europe. From S Greece (Taygetos Mts.) only recorded by Rebel (1902).

Throughout Turkey; south towards the Lebanon (BM), southeast through the mountains of Iraq and the Zagros Mts. to Fars (Wiltshire, 1957; Brandt, 1939). According to Romanoff (1884) south of the Caucasus widely distributed, but the distribution in N Iran is almost unknown, as the species is recorded by Alberti (1957) only from NE Iran.

In the Caucasus widely distributed (Wojtusiak & Niesiolowski, 1947; Alberti, 1969). Few records of the occurrence in S Russia: Gniliza (east of Charkow) (Alberti & Soffner, 1962), Crimea (Korshunov, 1964) and Sarepta (BM). In E Russia known from Uralsk, Guberli (BM), and Kasan (Krulikowsky, 1908). The records from Vologda and Kotlas (Krulikowsky, 1909) probably concern *P. alveus*.

East of the Urals possibly continuously distributed, but only recorded from the Tjumen district (Slavtchevsky, 1911), the Altai (Elwes, 1899), N Mongolia (Forster, 1965) and Jablonowyj Khrebet (= Apfelgebirge) (BM). Herz (1898) recorded the species from Vilui in NE Siberia, but it may be a misidentification for *P. alveus*.

Habitat. — More or less flowery places, clearings, meadows, etc., from sea level (W France, N Germany) up to 2400 m in the Spanish Pyrenees (Gerona; HC) and still higher in the Alps (Kauffmann, 1951); in Iraq from 1300 to 2000 m, in S Iran (Fars) above 2600 m (Brandt, 1939), in the Altai up to 2300 m (Elwes, 1899). Often in large numbers at damp places (mud and dung).

Biology. — Monovoltine; flight period, four to five weeks, date of emergence strongly influenced by altitude, in the lowlands from the middle of May, in Switzerland at 100 m from June, at high altitudes often from the middle of July (Warren, 1928; Kauffmann, 1951). The altitude appears to be more important for the flight period than the latitude: in N Germany adults from the middle of May to the middle of June (Friese, 1956). In Iraq bivoltine, flying in May and from July to October (Wiltshire, 1957).

The species hibernates in the larval stage (Koch, 1963).

Various species of *Potentilla* and *Alchemilla* (Rosaceae) have been recorded as food plants (Verity, 1940; Bergmann, 1952; Guillaumin, 1964). In addition, Verity mentioned *Aira montana* (Gramineae).

Geographic variation. — The sensitiveness to local conditions appears not only in the strong delay in the date of emergence in the mountains, but also in the variation in size, colour and design. This has led to the distinction of many "subspecies" even in cases where it is clear that the supposed subspecies is a climatic, non-hereditary form. Thus Kauffmann (1951: 349) says: "Die Zentraleuropäische Verhältnisse zwingen mich, neben den von Evans aufgestellten Unterarten noch die f. *planorum* Verity als Subspezies hinzuziehen" and he recognizes the subspecies *serratulae*, *caecus* and *planorum* in Switzerland. However, one page further he admits that *planorum* may be a climatic form: "Als Form ist *planorum* überall in der Schweiz zu finden mit anderen Formen vermischt, reichlicher in der Ebene und spärlicher im Gebirge. Sie ist wahrscheinlich die somatische Form von trockenem Klima" and he speaks of *caecus* in a similar manner. Even the great lumpner Evans (1949) thought it justified to recognize the subspecies *caecus*. As stated in Chapter 1.b it is not desirable to call climatic forms subspecies and therefore I recognize only a single subspecies in SW and C Europe.

In the eastern part of the range problems have arisen, due to the misleading lumping by Evans (1949) of different forms into the subspecies *uralensis*, and due to the abuse of the name *major* by various authors for forms which have little to do with the true *major* from Turkey (e.g. Higgins & Riley, 1970: 316—317: "Size varies, large specimens, f. *major* Staudinger Pl. 58 with fw 15/16 mm occur in lowlands in SW France and elsewhere (Vendée, Gironde, Charente, etc.) and in Balkans (esp. Greece)").

The following classification may be justified from the phylogenetic point of view.

***Pyrgus serratulae serratulae* Rambur**

Pl. 5 Fig. 73—76, 82—85

Material examined. — 702 ♂ 276 ♀: 149 ♂ 49 ♀ (Sierra Nevada and from Montes Universales and Sierra de Gredos to the Pyrenees) (BM, ML, ZMA, HC, RJ), 4 ♂ 3 ♀ Andorra (ZMA), 146 ♂ 65 ♀ French Pyrenees (Basses Pyrénées to Pyrénées Orientales) (BM, ML, ZMA, RJ), 179 ♂ 60 ♀ France (Alpes Maritimes, Basses Alpes, Hautes Alpes, Savoie, Cantal, Puy-de-Dôme, Ille-et-Vilaine, Auvergne, Vendée, Charente, Eure, Aube, Lozère, Seine-et-Marne, Bas-Rhin, Marne) (BM, ML, ZMA, RJ), 105 ♂ 39 ♀ Switzerland (Valais, Berne, Uri, Ticino, Grisons) (BM, ML, ZMA, RJ), 45 ♂ 23 ♀ Italian Alps (BM, ML, RJ), 9 ♂ 3 ♀ C Italy (BM, ZMA), 35 ♂ 20 ♀ Austria (Tyrol to Mödling) (BM, ML, ZMA, RJ), 14 ♂ 7 ♀ W Germany (northward to Niedersachsen) (BM, ML, RJ), 5 ♂ 1 ♀ Czechoslovakia (BM), 8 ♂ 4 ♀ Hungary (BM), 1 ♂ 1 ♀ Banat (ML), 2 ♂ 1 ♀ Bosnia (BM, ML).

Distribution. — W and C Europe; the zone of contact with the *major* subspecies group is not exactly known.

Subspecific characters. — Highly variable and, therefore, difficult to define. Small to large, ♂ 10.8—14.6 mm. Above, usually less spotted than in other subspecies. Below, spotting variable, usually less spotted than in other subspecies, unh the median spots 2 and 3 and the submarginal spots 3 and 7 usually faint or absent, rarely prominent. Rarely with clear white borders unf and unh. Colour unh dark olive-green to warm yellow.

Variation. — As stated above, highly variable according to local conditions. Some obvious variations are:

Forma *caecus* Freyer: small, ♂ 10.8—12.4 mm; above, spots very reduced, may be absent in female; below, colour faded, unh greyish-greenish with unsharp markings. This form is found almost everywhere above 2000 m in the Alps, together with specimens of the nominate form from which it cannot be well distinguished, as there seems to exist a continuous variation in the extension of the spotting. The ratio *caecus*: *serratulae* changes from year to year and depends on the climate (Kauffmann, 1951). It is, however, not confined to the Alps. Bergmann (1952) mentions the form from several localities in Thüringen (he attributes it to a cold and damp climate); other records are e.g. Caradja (1895): Poland. In addition, I saw some (rare) specimens from the Pyrenees.

Forma *serratulae* Rambur: somewhat larger, ♂ 11.6—13.2 mm; upf all spots of median row present, uph plain dark brown or more or less clearly spotted; unh cold greenish with clearly defined, somewhat reduced spots. Found in all mountain regions, varying towards f. *planorum* which is usually more common at lower altitudes.

Forma *planorum* Verity: slightly larger than *serratulae*, in Switzerland 12.8—13.7 mm (Kauffmann, 1951), but in France variable, may be as large as f. *magnagallicus*. Above,

spotted as in *f. serratulae*; unh various shades of a warm, yellowish colour; spots unh often more or less isolated and slightly rounded. Most numerous in the lowlands, but occurs everywhere with *f. serratulae*.

Forma *magnagalicus* Verity (= *occidentalis* Lucas). The specimens may be large, ♂ to 14.5 mm, in the northwestern part of the distributional area in France, from Vendée to Seine-et-Marne and Aube, otherwise like *f. planorum*. The variation from *f. planorum* to *f. magnagalicus* appears continuous; the males captured at Fontainebleau (Seine-et-Marne) vary from 13.2 to 14.5 mm.

The forms *diniensis* Heinrich and *arvernensis* Picard are not clearly defined local forms which fall within the variation of subspecies *serratulae*.

A large, *planorum*-like form, ♂ 12.8—13.9 mm, occurs in the Sierra de Gredos, upf well-spotted, unh spots reduced and colour of a strange, deep yellow shade.

major subspecies group

Evans (1949) united all forms east of Greece into a single subspecies, *uralensis*. He did not use the older name *major* Staudinger, 1879, as this name is preoccupied by *major* Fabricius, 1787 (= *Pyrgus carthami*). Warren (1926) described *uralensis* from two males and one female from Uralsk. I have seen nine males and four females from SE Russia. Although this is not a large number, I believe that *uralensis* is possibly a transitional form between the Turkish form (named *major* by Staudinger) and the Siberian form. But if the Ural and the Turkish forms are not identical, the Turkish form needs a new name. As it is not my intention to propose new names in the present paper, I only call attention to this case, further using the name *major* Staudinger.

Much less material is available concerning this subspecies group than concerning ssp. *serratulae*. Although there are clear-cut differences within the *major* subspecies group, it is possible that with more material becoming available, a part of the variation may prove to depend on climatic conditions only. Therefore, the following classification is provisional.

The group differs from ssp. *serratulae* by a usually large size, more extensive spotting upf, clearly defined white borders below, unh median row spots 2 and 3 and submarginal spots 3 and 7 usually well-developed. The spots of the median row unh isolated by ground colour along the veins and ground colour unh often greyish-powdered.

Usually, the specimens can easily be distinguished from specimens of ssp. *serratulae*, but the *major* group shows the same degree of variation as ssp. *serratulae*.

Pyrgus serratulae balcanicus Warren

Pl. 5 Fig. 77, 86

Warren, 1926 — Trans. ent. Soc. Lond. 74: 97—98; pl. 29 figs. 7—12.

Type-locality: Cetinje (Montenegro).

Material examined. — 24 ♂ 4 ♀ : 1 ♀ Montenegro (Cetinje) (BM), 13 ♂ 1 ♀ Yugoslavian Macedonia (BM, HC, RJ), 11 ♂ 2 ♀ Olympus (BM, ML).

Distribution. — Macedonia and Montenegro.

Subspecific characters. — Size variable, Yugoslavian Macedonia ♂ 13.7—14.8 mm, Olympus ♂ 14—15.5 mm. Upperside dark brown with little light superscaling (may be absent), upf spots well-developed, uph spots faintly visible. Unf dark grey or black,

white border narrow or obscure; unh dark brownish yellow with usually well-developed spots (on the average less extensive than in subspecies *major*) which are clearly isolated by the ground colour along the veins; white border unh narrow or obscure.

Note. — The name *infraobscuratus* Verity (1938) (type-locality: Mt. Olympus) is clearly a junior synonym of *balcanicus*. For some obscure reason Evans (1949) considered *balcanicus* a synonym of *serratulae* and *infraobscuratus*, a synonym of *uralensis*.

Pyrgus serratulae major Staudinger

Pl. 5 Fig. 78, 87

Staudinger, 1879 — Horae Soc. Entom. Ross. 14: 292.

Type-locality: Asia Minor.

Material examined. — 51 ♂ 13 ♀: 2 ♂ 1 ♀ Hungary (BM), 5 ♂ Bulgaria (Sliven) (BM), 2 ♂ Parnassus (BM), 22 ♂ 5 ♀ Turkey (BM, RJ), 1 ♀ Kasikoparan (BM), 20 ♂ 6 ♀ Syria (Akbès, Aintab) (BM).

Distribution. — From Greece and Bulgaria to Syria and Armenia.

Subspecific characters. — Large, ♂ to 16.1 mm. Upf with well-developed spots, often more extensive than in ssp. *balcanicus*, and with rather slight superscaling; uph spots rather faint; unf light to dark grey with obvious white border; unh spots large, isolated by ground colour along the veins, ground colour pale olive-greenish or yellowish (in worn specimens darker, owing to absence of light superscaling), in Syria sometimes dark brown, white border usually conspicuous, sometimes very narrow.

Variation. — The Hungarian specimens are about intermediate between ssp. *major* and ssp. *balcanicus*. As also ssp. *serratulae* is known from Hungary, more recent and more exact data are wanted.

The two males from Mt. Parnassus have less extensive spots unh and white border unh very narrow, thus resembling ssp. *balcanicus*.

Pyrgus serratulae alveoides Staudinger

Staudinger, 1901 — Cat. Lep. Pal.: 96.

Type-locality: Syria.

Material examined. — 7 ♂ 2 ♀ Lebanon (BM).

Distribution. — Lebanon and through the mountains of Iraq and the Zagros Mts., southward to N Fars (Wiltshire, 1957).

Subspecific characters. — Small, ♂ 12.4–13.3 mm; upf and uph strongly spotted and with obvious white superscaling; unf and unh with broad white border; spots unh variable, reduced to strongly developed; ground colour unh pale yellow or pale ochreous green. Ssp. *alveoides* differs in the male genitalia from other forms of the species in having a much more elongated cuiller, but transitional specimens also occur.

Pyrgus serratulae kotschi Alberti

Pl. 5 Fig. 79, 88

Alberti, 1957 — Mitt. Deutsch. Entom. Ges. 16: 27–28.

Type-locality: Kuh i Mirabi (NE Iran).

Material examined. — 2 ♂ Kuh i Mirabi (paratypes) (BA).

Distribution. — Only known from the type-locality. According to the original description, a similar form occurs in the Shahkuh Mts.

Subspecific characters. — Large, ♂ to 16 mm; above, spots small, uph faintly visible; below greyish; unh spots very large and more connected than in ssp. *major*, ground colour faded grey-olive; white borders below, obvious.

***Pyrgus serratulae grisescens* Alberti**

Pl. 5 Fig. 80, 89

Alberti, 1969 — Faun. Abh. Staatl. Mus. Tierk. Dresden 2: 141—142; figs. 3a—b.

Type-locality: Teberda (Caucasus).

Material examined. — 6 ♂ : 3 ♂ Teberda (NW Caucasus, 1700 m; paratypes), 3 ♂ Passanauri (Georgia, 1700 m) (BA).

Distribution. — Confined to the Caucasus.

Subspecific characters. — Size as in the Central European ssp. *serratulae*, ♂ 13.5 mm, above also recalling ssp. *serratulae*, but unh the large spots are *major*-like, although they are not as sharply isolated as in that subspecies; ground colour unh a peculiar shade of faded greenish grey (in worn specimens the colour may be darker owing to the absence of superscaling with light scales); white borders below narrow or absent.

***Pyrgus serratulae uralensis* Warren**

Pl. 5 Fig. 81, 90

Warren, 1926 — Trans. ent. Soc. Lond. 74: 98; pl. 29 figs. 1—6.

Type-locality: Uralsk.

Material examined. — 9 ♂ 4 ♀ : 1 ♀ Sarepta, 2 ♂ Guberli, 5 ♂ Ural (all BM), 2 ♂ 3 ♀ Uralsk (BM, ML).

Distribution. — SE Russia; but see also below, under Siberian form.

Subspecific characters. — Smaller than the Turkish ssp. *major*, ♂ 13—14.8 mm. Upperside and underside very much like ssp. *major*, the females indistinguishable from that subspecies, but the males variable: unh spots large and isolated to reduced and more coherent, a clearly defined white border along termen or the ground colour extending nearly or entirely to the termen. Upperside often more extensively spotted than ssp. *major*, particularly the spots uph may be conspicuous.

Note. — Although hampered by the limited number of specimens available, I still am of the opinion that *uralensis* is a hybrid population between the SE European and SW Asiatic form (ssp. *major*) and the Siberian form, some specimens being very much like ssp. *major*, other specimens being almost indistinguishable from specimens from the Altai. Therefore, I believe that the use of the name *uralensis* for the subspecies group is undesirable. I even doubt the usefulness of the subspecific distinction of *uralensis*, but the name can be provisionally used to indicate the hybrid population.

***Pyrgus serratulae* — Siberian form**

The Siberian populations of *P. serratulae* are poorly known. These are listed by Evans (1949) and Forster (1965) as ssp. *uralensis*. This attribution is not strange in view of the variation of ssp. *uralensis* described above, but on the whole, Siberian specimens show so little resemblance with subspecies of the *major* group, that they should be

excluded from the *major* group and be considered to belong to a separate subspecies. This Siberian form will remain unnamed for the present in view of the limited number of specimens available.

Material examined. — 9 ♂ 5 ♀: 8 ♂ 1 ♀ Altai (Ongodai, Tchuja Valley), 1 ♂ 4 ♀ Jablonowyj Khrebet (= Apfelgebirge) (BM).

Distribution. — Presumably from the Urals to E Siberia.

Subspecific characters. — Altai ♂ 13—14.3 mm, Jablonowyj Khrebet ♂ 12.7 mm. Upperside more extensively spotted than ssp. *major*, particularly uph, but less than ssp. *alveoides*; unh recalling ssp. *uralensis*, spots not as reduced as in some specimens of ssp. *uralensis*, hardly or not at all intersected by the ground colour.

Geographic history. — Although the material available from Siberia is very limited, there seems to exist little variation, particularly in comparison with the situation in SE Europe and W Asia. This suggests that the occurrence of the species in Siberia is of a more recent age than the occurrence in SE Europe and W Asia, also because of the absence of closely related species in Asia. The slight variation in Siberia also points to the assumption that the Siberian form arose from a single, geographically isolated population in S Siberia, possibly during the Last Glacial. The W Siberian lowlands may have become inundated during the Last Glacial (cf. Moreau, 1955), in this way isolating the Siberian populations from the more western ones. Thus the geographically as well as morphologically intermediate position of ssp. *uralensis* becomes understandable, as these populations apparently met postglacially, giving rise to a zone of secondary intergradation.

Ssp. *major* evidently originated in a refugium in SE Europe or SW Asia during the Last Glacial. It is at present impossible to be exact on the extension of this refugium, whether it was restricted to Asiatic Turkey or also included Greece (and S Russia?), but apparently it was situated north of the region where ssp. *alveoides* originated. There is no reason to date the origin of ssp. *alveoides* further back than in the Last Glacial or at best in the Third Interglacial. In a Glacial (Pluvial) rather than in an Interglacial Period it may have had ample opportunity to extend its range, but I rather do not infer the history of ssp. *alveoides* without having seen specimens from the Zagros Mts.

Ssp. *kotzschii* is possibly an extreme, postglacially developed form of ssp. *major*, but the entirely unknown situation in NW and N Iran makes a reliable conclusion impossible. Likewise, ssp. *grisescens* may be a postglacial descendant from ssp. *major*, but it may equally well have originated in an isolated area during the Last Glacial.

The characters of ssp. *balkanicus* seem to be too constant to conclude that this subspecies is only a product of postglacial hybridization of the subspecies *major* and *serratulae*. Evidently it had a refugium of its own during the Last Glacial.

Subspecies *serratulae* presumably arose in a refugium in Spain and (or) Italy, during the Last Glacial. From the present geographic variation it is not possible to infer that the subspecies occurred in W Europe during and before the Third Glacial, but of course this is not impossible.

So we cannot trace the history of the species far back. It is interesting to note that the species is evidently a western immigrant in Siberia.

14. *Pyrgus onopordi* Rambur

Rambur, 1839 — Faune entom. de l'Andalousie: pl. 8 fig. 13, p.

Type-locality: Granada.

Distribution (Map 12). — NW Africa and SW Europe. In NW Africa widely distributed, from S Morocco to E Algeria in High Atlas, Middle Atlas and Tell Atlas (BM, RJ). Throughout Portugal and Spain, but absent in NW Spain (Agenjo, 1952). The species is widely distributed throughout S France: I have seen specimens or reliable records from the following departments: Basses Pyrénées (HC), Hautes Pyrénées (Verity, 1947; BM), Pyrénées Orientales (Dufay, 1961), Tarn (RJ), Lot (BM), Charente (BM), Vienne (BM), Gard (Picard, 1948c; Gaillard, 1952), Bouches-du-Rhône (Verity, 1947; BM, ML), Vaucluse (ZMA), Var (BM), Alpes Maritimes (Verity, 1947; BM, RJ), Basses Alpes (Verity, 1947; various collections), Hautes Alpes (BM, RJ), Savoie (BM). Throughout Continental and Peninsular Italy (Verity, 1940); recorded by Schwingenschuss (1942) from Sicily, (possibly a misidentification); apparently absent from Corsica and Sardinia. In Switzerland only in Valais and the Grisons (Kauffmann, 1951). Apparently absent east of the Adriatic Sea, apart from the records by Warren (1926) from Bosnia and Kronstadt (Rumania).

Habitat. — Flowery and usually dry localities, meadows, waysides, etc. in the lowlands, in Switzerland rarely above 1000 m (Kauffmann, 1951), in Morocco, however, up to 2700 m (Djebel Anngour; RJ); caught at the same height in the Sierra Nevada by Manley & Allcard (1970).

Biology. — Bi- or trivoltine; flight period in Switzerland from April to October (Kauffmann, l.c.).

The larvae have been reared by Powell in N Africa on *Malope malachoides* (Malvaceae) (cf. Guillaumin, 1964).

Geographic variation. — The variation of this rather variable species has been discussed by Verity (1925) in his well-known erratic way, giving many new names rather than making the variation surveyable. He recognized four "races" and, in 1947, he even mentioned five "races" in France alone. I find it impossible to define subspecies of this species. The variations may be described as follows.

The first generation is largest in N Africa and many Spanish localities, ♂ 12.2–14 mm, smallest in the Alps, ♂ 12–12.5 mm. Spots above variable, smallest in the Alps, where the ground colour is rather pale. Ground colour unh in various shades of greenish or ochreous grey or fulvous to warm reddish fulvous, more or less overlaid by dark scales. The colour seems to depend on microclimatic conditions. In a series of eight males from the Djebel Anngour district (High Atlas), 2700 m, June, the colour varies from a very warm reddish ochreous with slight dark superscaling to an evenly darkened cold greyish-green. In the Alps the colour is pale greyish-green with less contrasting white spots. Particularly in N Africa, but also elsewhere, the white spots unh are often outlined by capillary black streaks. These streaks are generally absent in specimens from dry localities in Italy and S France.

The ground colour unh in the second generation is in general yellowish or fulvous, more or less overlaid by dark scales; usually of a warmer tinge than in the first generation, sometimes very vivid reddish fulvous. In some specimens from the Alps the ground colour unh is cold pale greenish grey, the same as in the first generation. About as large as the first generation, in the Alps usually a little smaller, ♂ 10.6–12.2 mm.

A possible third generation is differing not much from the second generation.

We may summarize the variation as follows: the higher the temperature (north to south, high to low, spring to summer), the warmer the colour. Local differences can obviously complicate this general picture.

The difference between pale greenish grey and warm fulvous is not as great as one would suppose at the first sight. It is only due to the intensity of the pigmentation of the yellow scales, combined with the intensity of the dark superscaling. Pale yellow scales, suffused by few dark scales give the impression of pale greenish grey, dark yellow scales with many dark scales give a brownish tinge, etc.

For the particulars of microclimatic, rather than geographic, forms may be referred to Verity (1919, 1925, 1928, 1940), who is the author of twelve of the fifteen names, given to varieties of this species. Here, only the name of the extreme form of the Alps is mentioned, as it is often used in literature: *conyzae* Guenée. This form is, however, not confined to the Alps; I have seen specimens from Septèmes near Marseille which are indistinguishable from first brood specimens from the Alps, while the more frequently occurring form of Septèmes is larger and unh warm ochreous.

Material examined. — 322 ♂ 227 ♀: 39 ♂ 29 ♀ Morocco (BM, RJ), 54 ♂ 54 ♀ Algeria (BM), 39 ♂ 22 ♀ Spain (BM, ML, ZMA, RJ), 7 ♂ 7 ♀ Portugal (BM), 142 ♂ 86 ♀ France (Basses Pyrénées, Hautes Pyrénées, Vienne, Charente, Lot, Tarn, Bouches-du-Rhône, Vaucluse, Var, Alpes Maritimes, Basses Alpes, Hautes Alpes, Savoie) (BM, ML, ZMA, HC, RJ, HO), 2 ♂ 5 ♀ Switzerland (Valais) (BM, ML), 4 ♂ 2 ♀ N Italy (ML, ZMA, RJ, HO), 35 ♂ 22 ♀ C Italy (BM, ML, ZMA).

Geographic history. — The origin as well as the geographic history of the species is entirely obscure.

15. Superspecies *Pyrgus carlinae* Rambur

Taxonomy. — Until Picard's publication in 1950, *carlinae* and *cirsii* were considered separate species, as they differed constantly in facies and genitalia. Picard (1950b) found in the French Alps intermediate specimens almost as numerous as typical specimens, particularly in La Bessée (Hautes Alpes), but he did not give exact data. Kauffmann (1951, 1954b) could not decide on conspecificity, although he knew Picard's paper. Virtually the only reason for Kauffmann's considering *carlinae* and *cirsii* separate species was that they differ elsewhere. In this, as well as in other cases it is apparent that the biological species concept was beyond this author. Apparently, Picard estimated the number of intermediates too high. Guillaumin (1964) mentions a score of 14 % intermediates in the localities where *carlinae* and *cirsii* come into contact (Hautes Alpes: La Bessée, Le Lautaret). Additional studies are still in progress (Guillaumin, in litt.). For the present study the most important fact is the interbreeding, as it indicates an incomplete stage of speciation. Contact between the lowland form *cirsii* and the mountain form *carlinae* is only known from the French Alps. Apparently, they interbreed wherever they have contact. It is nonsensical to consider them separate species. I prefer to call *carlinae* and *cirsii* semispecies, as members of the same superspecies, thus indicating the supposed, rather progressed stage of speciation. But of course, it is also tenable to call them subspecies of a single species, see also Chapter 1.b. The decision is not important for the present study.

Biologically the hybridization between *P. carlinae* and *P. cirsii* is interesting as *P. carlinae* hibernates in the egg stage and *P. cirsii* in the larval stage (see Guillaumin, 1964).

Externally *P. carlinae* and *P. cirsii* can easily be distinguished by the more square-shaped and much larger spots upf and the better marked uph in *P. cirsii* (see also Kauffmann, 1954d). In the male genitalia differences can be found in the lateral apophyses (four to six unequal teeth in *P. carlinae*, more than six, more or less equal, teeth in *P. cirsii*) and in the subharpal plate (united to the harpe in *P. carlinae*, not united in *P. cirsii*). In the female genitalia the antevaginal region is sclerotized in *P. carlinae*, membranous in *P. cirsii*. Good figures can be found in Warren (1926), Opheim (1956) and Guillaumin (1964, 1966).

Distribution (Map 13) and biology. — Mainly confined to Europe: *P. carlinae* only in the western and southwestern Alps, usually from 1500 m upward, *P. cirsii* mainly in the lowlands, rarely at 1500 m or higher, in SW Europe, but also found in E Turkey.

Both semispecies are monovoltine, flying from July to September. As far as known, both live on *Potentilla verna*.

Geographic history of the superspecies. — The hybridization between *P. carlinae* and *P. cirsii* indicates a recent history of the superspecies and Picard (1950b) may be correct in supposing that *P. cirsii* originated during the Last Glacial in a Spanish refugium and *P. carlinae* in S France. However, *P. cirsii* may have a much wider distribution in E Europe than we can conclude from the present data and we do better not to speculate on refugial areas as long as the distribution of *P. cirsii* is insufficiently known. Although it is still difficult to understand in what way the differentiation into the cold-adapted *P. carlinae* and the warmth-loving *P. cirsii* took place, it is interesting to note the short time, probably necessary for such an extreme ecological differentiation.

P. carlinae seems to have more primitive characters: the fusion of harpe and subharpal region and the genital plate. This is important for assuming phylogenetic relations, but it does not mean that the ancestor of *P. carlinae* and *P. cirsii* was adapted to high altitudes. It may have been more eurytherm than the present semispecies. In this connection it is important to note that *P. cirsii* may fly at higher altitudes in regions where *P. carlinae* is absent (Pyrenees, E Turkey).

Virtually the history of the superspecies is very obscure. It is hard to say how far the contact between *P. carlinae* and *P. cirsii* may have been stimulated by human agency (deforestation).

15.a. *Pyrgus carlinae* Rambur

Rambur, 1839 — Faune entom. de l'Andalousie: pl. 8 figs. 11, 12.

Type-locality: Alps.

Distribution (Map 13). — Confined to the western and central Alps, from the Alpes Maritimes to Engelberg (C Switzerland) and Tomsee (Ticino). According to Kauffmann (1954b), records of more eastern localities are based on misidentifications (or on false data). This is quite possible but the fact that Kauffmann had not seen specimens from more eastern localities cannot be a definitive proof for the absence of the species in the eastern part of the Alps.

Habitat. — Alpine meadows, often abundant in damp places; usually from 1500 m upward (Guillaumin, 1964), in Switzerland from 1000 m upward, occasionally as low as 700 m (Kauffmann, 1951). According to Verity (1940) in Savoie up to 3200 m.

Biology. — Monovoltine; flight period from the middle of July to the beginning of September (Kauffmann, 1951).

Food plant, *Potentilla verna* (Rosaceae) (Verity, 1940; Guillaumin, 1964); according to Kauffmann (1954c) also other species of *Potentilla* are probably accepted as food plant by the larvae.

The species hibernates as egg (Kauffmann, l.c.; Guillaumin, l.c.).

Geographic variation. — The species is rather variable, particularly in the colour unh which can be red, brown, ochreous yellow or greenish. Kauffmann (1951, 1954b) recognized four subspecies based on size, extension of the spots above and colour unh: *carlinae* (type-locality: Alps), *atratus* Verity (type-locality: Vaud, Switzerland), *ochroides* Kauffmann (type-locality: C Alps) and *cottianus* Kauffmann (type-locality: Cottian Alps). The species appears to be rather sensitive to differences in microclimate, resulting in a high local variability. Therefore it is not surprising that the four subspecies recognized by Kauffmann are not clearly defined and overlap to a great extent in their characters. The variation appears to be clinal, at least as far as the colour unh is concerned; it can be described as follows:

In the S Alps (Alpes Maritimes, Basses Alpes) the colour is reddish, red-ochreous or, more frequently, bright ochreous to yellow-ochreous. More to the north the red colour disappears. In the Cottian Alps the colour varies from light brownish ochreous to olive-brown, the veins being clearly outlined by lighter scales especially in the darker specimens. Still further north, in the Val d'Aosta and throughout the Swiss localities the colour is still darker and a reddish tinge is absent, the veins are clearly contrasting with the ground colour; many specimens, however, are not darker than specimens from the Cottian Alps.

Small specimens with reduced spotting above and greenish unh may occur everywhere with other forms; they are perhaps most common in the northwestern part of the range.

It does not appear useful to divide this variational pattern into subspecies.

Material examined. — 354 ♂ 107 ♀: 37 ♂ 2 ♀ Alpes Maritimes (St. Martin de Vesubie) (BM), 33 ♂ 3 ♀ Basses Alpes (BM), 58 ♂ 17 ♀ Hautes Alpes (BM, ZMA, RJ), 26 ♂ 26 ♀ Savoie (BM), 97 ♂ 40 ♀ Valais (BM, ML, ZMA, RJ), 19 ♂ 5 ♀ rest of Switzerland (BM, ML, ZMA, RJ), 75 ♂ 9 ♀ Val d'Aosta (BM, ZMA, RJ), 7 ♂ 1 ♀ Piedmont (BM), 2 ♂ 4 ♀ Tirol-Carinthia (BM).

Geographic history. — See the history of the superspecies.

15.b. *Pyrgus cirsii* Rambur

Rambur, 1839 — Faune entom. de l'Andalousie: pl. 8 figs. 12, o.

Type-locality: Fontainebleau.

Distribution. (Map 13). — SW and C Europe. According to Manley & Allcard (1970) distributed throughout the Iberian Peninsula, but reliable records of the occurrence in Portugal have not been found by the author. Throughout the greater part of France, north to approximately 49° N Lat. (Verity, 1947). In Switzerland found only in the Jura. In W Germany north to approximately the northern boundary of Bavaria, especially between the Danube and the Main (Alberti, 1927). Further east very incompletely known, partly due to the fact that the species has long been classified as a variety of *Pyrgus alveus*, and to the fact that the name *fritillum* Schiff. has frequently been used for this and for other species. According to Verity (1947), near Vienna, particularly west of the city. Warren (1926) even mentioned Sofia.

Very surprisingly, De Lattin (1950) recorded the species from E Turkey (west side of Van Lake) and Alberti (1969) added an other locality in E Turkey (Göle, in the Vilayet Kars). These discoveries suggest a much wider distribution of the species in SE Europe than at present known.

Habitat. — Dry, flowery places, usually at low altitudes, in the Swiss Jura not above 1200 m (Kauffmann, 1951), in the French Alps up to 1500 m and in the Pyrenees up to 2000 m (Guillaumin, 1964). Recorded in Spain between 900 and 1750 m (Manley & Allcard, 1970) and in E Turkey between 2300 and 2600 m (Alberti, 1969).

Biology. — Monovoltine; flight period in the Swiss Jura from the end of July until the beginning of September (Kauffmann, 1951). Manley & Allcard (1970: 14), however, stated: "There are two generations each year, but we have found the species only in July and August". Their record of two generations is undoubtedly copied from Verity (1925), but I have not been able to find any indications of more than a single brood per year.

Food plant: *Potentilla verna* (Rosaceae) (Guillaumin, 1964). According to this author the species hibernates in the larval stage, but it is not known whether this is also the case at higher altitudes.

Geographic variation. — As in *P. carlinae* the variation of *P. cirsi* seems to be clinal in a north-south direction. The specimens in Spain (*ibericus* Gr.-Gr. = *fabressei* Obth.) are usually large, ♂ to 14.7 mm, with extensive spotting and colour unh ochreous to a warm fulvous or reddish, slightly overshadowed by darker scales (usually in patches). In addition, smaller specimens with darker unh (more saturated with dark scales) occur throughout Spain; I have seen such specimens from as far south as Sierra de Alfacar.

In S France the specimens are usually smaller; in a series of 18 males from Bagnols-les-Bains (Lozère) the largest male was 13.1 mm; but in other places the specimens may be as large as in Spain, e.g. Luberon (Var) ♂ to 14.5 mm. The colour unh is variable, often darker, with a deeper red, than the colour in Spanish specimens, but sometimes also ochreous in various tinges. The smaller and deeper tinged French form was named *parafabressei* by Verity who (1925, 1947) stated that the *ibericus*-like specimens in S France are confined to the hottest and driest localities. The specimens from N France to C Europe are still smaller, ♂ to 13 mm, but often smaller, with dark underside, unf deep black, unh strongly overlaid by dark scales to a brown or greenish colour, but *parafabressei*-like specimens also occur. This is the nominate form. A form occurs in the northern part of the Swiss Jura which was named *tramelensis* by Kauffmann (1951), and which is characterized a.o. by the absence of a reddish tinge unh. I have not seen specimens from that region, but the description agrees very well with many French specimens. There is therefore no reason for the separation. Apart from this the name *tramelensis* may be synonymous with *nigrocarens*, given by Verity (1925) to a specimen from Tramelan (figured by Reverdin, 1910), but Verity left it an open question whether this is a race or an individual variation. Specimens with a cold greyish-greenish unh, named *herrichii* by Oberthür (1910) occur throughout the range of the species.

The distribution of the various forms suggests that the variation is clinal and largely or entirely due to microclimatic differences.

The five males and the two females from NE Turkey do not differ constantly from a series from Pottenstein (north of Nürnberg) (Alberti, 1969). However, De Lattin (1950) described the subspecies *turcivola* on a single male, adding to his description: "Eine grosse Rasse (Vfllänge 10 mm), die infolge ihrer intensiven Weisszeichnung auf

den ersten Blick os stark von der gewöhnlichen *fritillum* der westlichen Fluggebiete abweicht, jedoch im Genitale (Abb. 8) nicht von ihr zu unterscheiden ist, und die daher zweifellos als östliche Vikariante zu dieser Art gezogen werden muss" (p. 326). According to my measurements a fore wing length of 10 mm cannot be considered large, but very small instead. For the rest, bold statements based on a single specimen should be avoided.

Material examined. — 275 ♂ 109 ♀ : 75 ♂ 39 ♀ Spain (Andalusia, Old Castille, New Castille, Aragon, Catalonia) (BM, ML, ZMA, RJ), 2 ♂ 2 ♀ Andorra (BM), 186 ♂ 64 ♀ France (Ariège, Haute Garonne, Lozère, Bouches-du-Rhône, Vaucluse, Var, Alpes Maritimes, Basses Alpes, Hautes Alpes, Charente, Lot, Dordogne, Puy-de-Dôme, Saône-et-Loire, Haute Savoie, Loire Inférieure, Eure-et-Loire, Yonne, Seine-et-Marne, Doubs, Bas-Rhin) (BM, ML, ZMA, RJ), 5 ♂ Switzerland (Vaud) (BM), 7 ♂ 3 ♀ W Germany (Nürnberg, Fürth, Dillingen) (BM, RJ), 1 ♀ Austria (ML).

Geographic history. — See the history of the superspecies.

16. *Pyrgus cinarae* Rambur

Rambur, 1839 — Faune entom. de l'Andalousie: pl. 8 figs. 4, 5, j.

Type-locality: Sarepta.

Distribution (Map 14). — Discontinuously from Spain to Turkestan. In Spain only recorded from the Montes Universales (C Spain) (cf. Manley & Allcard, 1970), but in the BM there is a female from Sierra de Alfacar in S Spain, collected by Ribbe.

The species is widespread in Macedonia (Turner, 1964), which is the nearest place to Spain, where it has been collected. Further in the Balkans only known from Sliven (Bulgaria) (Rebel, 1903; see also Material examined). In Turkey widely, but evidently locally spread. According to Staudinger (1881) near Brussa, in Pontus and in Lydia; in addition Warren (1926) mentioned Kurdistan and Wagner (1929), Aksehir; see also Material examined. From S Russia only few records: apart from specimens in various collections labelled "S Russia", there are specimens from Sarepta and Guberli in the BM, whereas Alberti & Soffner (1962) recorded the species from the eastern Denez region. In the BM there is also a male labelled "Turkestan", but I doubt the label as no other specimens from that region seem to be known.

Habitat. — Dry, hot localities with scarce vegetation, steppes, mountain slopes, in Macedonia up to the timber line (Turner, l.c.).

Biology. — Unknown.

Geographic variation. — There is a slight geographic variation in the colour unh. Warren (1927) described the Spanish form under the name *clorinda*, based on the following characters: ground colour unh bright yellow with veins outlined in light yellow; spots uph slightly buff or cream in the male and of a deep, almost ochre, shade in the female. According to Warren "the effect is very much more striking than the description would lead one to suppose" (p. 81). Virtually the difference between specimens from Spain and from the eastern Mediterranean is very slight: some eastern specimens are indistinguishable from Spanish ones.

It is only a matter of taste whether one regards the Spanish form as a subspecies or not. That an isolated population is different, is not surprising, but it is interesting that in this instance the difference is so slight. This does not need to be an objection against a subspecific separation.

Pyrgus cinarae clorinda Warren

Warren, 1927 — Ent. Rec. 39: 81—82.

Type-locality: Tragacete, Villacabras (Cuenca).

Material examined. — 5 ♂ 1 ♀: 2 ♂ Tragacete, 2 ♂ Huelamo, 1 ♂ Villacabras, 1 ♀ Sierra de Alfacar (all BM).

Distribution. — C (and S?) Spain.

Subspecific characters. — See above.

Pyrgus cinarae cinarae Rambur

Material examined. — 87 ♂ 17 ♀: 7 ♂ 1 ♀ Macedonia (Skopje, Naussa, Seli, Ohrid, Petrina planina) (BM, ML, RJ), 24 ♂ Bulgaria (Sliven) (RJ), 33 ♂ 9 ♀ Turkey (Kedos, Aksehir) (BM, RJ), 22 ♂ 7 ♀ S Russia (Sarepta, Guberli, "S Russia") (BM, ML), 1 ♂ Turkestan (BM).

Distribution. — From Macedonia eastward.

Subspecific characters. — Ground colour unh varies from yellow to dull olive-green; spots uph in male often cream-coloured, in female always somewhat more darkened.

Geographic history. — The slight difference between Spanish and E Mediterranean specimens suggests that the discontinuity in the distribution is of a recent age, presumably Postglacial, but it is also possible, that it is only a reflection of a stable gene configuration or of stable habitat circumstances. In the first mentioned case the species may have spread to Spain during the Boreal or Atlantic climate phase, in the other cases it is possible that the Spanish population is a relic of a continuous Mediterranean distribution in the Third Interglacial. Thus, the reconstruction of the history of *cinarae* is highly unsatisfactory, but it seems closely connected with the history of the fauna of the dry and warm mountain slopes of the Mediterranean.

17. *Pyrgus armoricanus* Oberthür

Oberthür, 1910 — Ét. Léop. Comp. 4: 411; pl. 57 figs. 509—517.

Type-locality: Rennes (W France).

Distribution (Map 15). — West Palaearctic. From NW Africa through S and C Europe to SE Russia and NE Iran (see below, Material examined). In NW Africa only recorded from the Middle Atlas in Morocco and Algeria (Picard, 1950d; Higgins & Riley, 1970). The northern distribution limit runs through Belgium (cf. Lempke, 1953) and N Germany (Urbahn, 1939; Alberti, 1940; Friese, 1956). A few localities still further north are known: in Denmark in N and W Seeland, Jutland (a single specimen) and Bornholm (Wolff, 1939) and in Sweden in the extreme south (Scania: Benestad, Sandhammaren, Löderup: Nordström, Opheim & Valle, 1955). The northern limit further eastward is very badly known, partly due to a possible confusion with *Pyrgus alveus*. The northernmost locality in Russia from where I have seen a reliable record, is Tula (Warren, 1926). The species is wide-spread in S Russia (Alberti & Soffner, 1962).

In Iran southward to Shiraz (Brandt, 1939) and eastward to the Achal Tekke region (BM), apparently restricted to the mountains, as in Iraq (Wiltshire, 1957). Through W Syria southward to the Lebanon.

Habitat. — Flowery and often dry places, in S Russia in the steppes and even in the

semi-desert (Alberti & Soffner, 1962); most common in the lowlands. In Switzerland and Italy infrequently above 600 m and very rarely at 1200 m (Verity, 1940; Kauffmann, 1951), in Iraq restricted to the mountains, from 1300 to 2000 m (Wiltshire, 1957).

Biology. — Bivoltine, but a partial third brood occurs at least in Italy; flight periods mainly May—June and August—September, but specimens have been found in the Mediterranean region during all months from February to October (Warren, 1926). In Iraq adults of the two generations occur in May and July—October respectively (Wiltshire, 1957).

Females depositing eggs on *Fragaria vesca* and *Potentilla reptans* (Rosaceae) have been observed by Rehous (in Reverdin, 1912) and on *Potentilla verna* by Picard (1950c). Rehous reared the larvae until the beginning of November and as they were still far from full-grown at that time, it is highly probable that *P. armoricanus* hibernates as larva.

Geographic variation. — The male genitalia vary geographically with regard to the shape of the apex of the cuiller: this apex is sharply pointed and the free proximal edge of the cuiller is concave in the western populations (west of the Balkans) (*armoricanus* type); in the eastern populations the apex is blunt and the free proximal edge of the cuiller is more or less straight (*persicus* type). The blunt apex has not been found west of the Balkans, but the pointed apex has been found in many parts of the eastern range of the species, in the Balkans, in Turkey and in Iran. This has been known since long (Reverdin, 1916; Warren, 1926; Alberti, 1940), but records concerning the proportion of both forms are lacking. The blunt apex apparently predominates in the southeastern Balkans and further eastward. I examined the genitalia of 103 males from the eastern part of the range of the species and found the following proportions:

locality	number examined	<i>armoricanus</i> type	number transitional	<i>persicus</i> type
Hungary	10	8	1	1
Croatia	6	6		
Bosnia	2	1		1
Dalmatia	7	2	3	2
Montenegro	1		1	
Macedonia	3		1	2
N Greece (Olympus-Saloniki)	17		7	10
Bulgaria	7	2	1	4
Rumania	1			1
Bosphorus	5	1	1	3
Turkey	30	1	3	26
Armenia	1			1
Georgia	1			1
Syria	1			1
Lebanon	4			4
Iran (Elburz Mts)	1		1	
Achal Tekke	2		1	1
S Russia (Zymljanskaja)	4			4

It is, of course, often difficult to call a structure "transitional", but even if we list all specimens considered transitional as *armoricanus*, then still is the predominance of the *persicus* type of cuiller in specimens collected east of the Balkans evident. Within these two groups (*armoricanus* and *persicus*) various forms have been described as subspecies but at least some of these belong to the ecophenotypic variation (e.g. *cacaoticus*). The following classification has to be considered provisional, but this is not very important for the reconstruction of the geographic history of *armoricanus*.

armoricanus subspecies group

Differs from the *persicus* subspecies group only in the sharply pointed apex of the cuiller.

Distribution. — The western part of the range of the species, eastward to Hungary and the northern Balkans. Perhaps much further east, as Warren (1926) recorded a male from Tula in C Russia with genitalia intermediate between *armoricanus* and *persicus*.

Pyrgus armoricanus maroccanus Picard

Picard, 1950 — Bull. Soc. Sci. nat. Maroc 28: 110.

Type-locality: Morocco.

Material examined. — 29 ♂ 10 ♀ : 16 ♂ 7 ♀ Morocco, 13 ♂ 3 ♀ Algeria (BM).

Distribution. — Morocco and Algeria.

Subspecific characters. — Rather large, ♂ 13—14.2 mm, with large and obvious spots above, also uph.

Note. — A slightly differentiated form, indistinguishable from some specimens from Spain, S France and C Italy.

Pyrgus armoricanus armoricanus Oberthür

Material examined. — 386 ♂ 167 ♀ : 50 ♂ 14 ♀ Spain (BM, RJ), 194 ♂ 109 ♀ France (BM, ML, ZMA, RJ), 2 ♀ Belgium (ML), 2 ♂ 1 ♀ Germany (Kreuznach, "Germany") (BM, ML), 19 ♂ 7 ♀ Switzerland (BM, ML, ZMA), 14 ♂ 4 ♀ Austria (BM, ML, RJ), 57 ♂ 4 ♀ Italy (BM, ML, ZMA, RJ), 15 ♂ 7 ♀ Sicily (BM), 6 ♂ 6 ♀ Corsica (BM), 3 ♂ Istria (RJ), 12 ♂ Croatia (BM), 14 ♂ 13 ♀ Hungary (BM).

Distribution. — European part of the range of the *armoricanus* subspecies group, eastward to C Germany.

Subspecific characters. — A variable subspecies. ♂ 11.3—14.2 mm. Above spots variable, usually smaller than in the subspecies *maroccanus* and *disjunctus*, suffusion with light scales usually not very pronounced.

Variation. — The first generation, and in the north (from C France northward) also the second generation, have usually a dark upperside, with rather small spots upf and indistinct spots uph (submarginal spots often partly absent). This probably ecophenotypic form occurs at the type locality of subspecies *armoricanus*. In southern regions specimens of the second brood are often suffused with yellow above and more frequently than in

the first brood with a tawny unh (*fulvoinspersus* Verity, 1919 = *siciliae* Oberthür, 1913). According to Verity (1940) this form occurs in relatively dry localities. The first and the second brood under relatively humid conditions are characterized by a rather large size, a black ground colour unh and a dark greenish or brownish ground colour unh (*cacaoticus* Verity, 1929). In the second brood also specimens occur with a vivid reddish ground colour unh (*rufosaturus* Verity, 1925 = *corsicus* Oberthür, 1919, see Picard, 1949d). In southern regions the specimens are often better marked above, especially unh, than in the north, but much variation occurs. I regard the above forms as ecophenotypic variations of the subspecies.

According to Alberti (1940), the Hungarian populations can be referred to subspecies *disjunctus* but the Hungarian specimens examined by me may equally well be listed as subspecies *armoricanus*. It may be recalled that of the ten males from Hungary of which I examined the genitalia, one has the *persicus* type of cuiller and one is intermediate between *armoricanus* and *persicus*. This means that the influence of *persicus* is perceptible as far north-west as Hungary. The Hungarian populations can be listed as ssp. *armoricanus*, as the influence of *persicus* appears to be small.

The subspecific status of S German populations is unclear, probably as a result of lack of material, but also of the slight degree of differentiation between the subspecies *armoricanus* and *disjunctus*. Alberti (1940) regarded the S German populations as ssp. *armoricanus*, but Kauffmann (1951) listed the populations of S Bavaria as ssp. *disjunctus*.

Pyrgus armoricanus disjunctus Alberti

Alberti, 1940 — Mitt. Münch. Ent. Ges. 30: 252; pl. 2 figs. 4-c, 7-a.

Type-locality: Halle.

Material examined. — 5 ♂ 2 ♀ : 1 ♂ Giessen (ML), 2 ♂ 2 ♀ Halle, 1 ♂ Praha, 1 ♂ Bohemia (all BM).

Distribution. — The northern part of C Europe; from C Germany and Czechoslovakia northward. Alberti (1940) also assumed that the Hungarian population and even the Algerian belonged to this subspecies.

Subspecific characters. — Small, ♂ 11–12 mm; above with large and conspicuous spots, also unh, and strong suffusion with light scales; below also with large spots, ground colour unh greyer than in ssp. *armoricanus*.

Note. — Small specimens can be found throughout the range of the species. Some of these are indistinguishable from specimens from C Germany. Specimens in W Germany (Kreuznach; see above, under ssp. *armoricanus*), Belgium, N France and Styria are often not larger than ssp. *disjunctus* but have smaller spots.

Ssp. *disjunctus* is probably rather constant in its distribution range. The differentiation is slight with regard to the variability of ssp. *armoricanus*.

persicus subspecies group

Characterized by the blunt apex of the cuiller. It is impossible to distinguish this subspecies group on the basis of external characters.

Distribution. — The eastern part of the range of the species, east of the northern Balkans.

I include the populations of Bosnia, Dalmatia and Bulgaria in this subspecies group, although these could be listed as ssp. *armoricanus* as well (see above).

Pyrgus armoricanus persicus Reverdin

Reverdin, 1913 — Bull. Soc. Léop. Genève 2: 218—224; pl. 21 fig. 4; pl. 22 fig. 9.

Type-locality: KuldSar (Iran).

Material examined. — 151 ♂ 52 ♀: 2 ♂ Bosnia (RJ, ZMA), 7 ♂ 1 ♀ Dalmatia (BM, RJ), 1 ♂ Montenegro (BM), 3 ♂ Yugoslavian Macedonia (RJ), 49 ♂ 21 ♀ Greece (BM, ML, ZMA), 8 ♂ 1 ♀ Bulgaria (BM, ML), 1 ♂ Rumania (BM), 35 ♂ 9 ♀ Bosphorus (BM), 33 ♂ 8 ♀ Turkey (BM, RJ, ML), 1 ♂ Armenia, 1 ♂ Georgia, 5 ♂ 2 ♀ S Russia (Zymljanskaja, Novorossiisk), 1 ♂ 3 ♀ N Syria, 1 ♂ 3 ♀ W Iran, 1 ♂ 4 ♀ Elburz Mts., 2 ♂ Achal Tekke (all BM).

Distribution. — As that of the *persicus* subspecies group, except the Lebanon.

Subspecific characters. — Very variable. ♂ 12—14 mm; usually well spotted above; ground colour unh ochreous to greenish.

Variation. — Pfeiffer (1927) described the Anatolian population as *prostanae*, differing from the Iranian form in the larger spots above and the greenish ground colour unh. Neither of these characters, however, is confined to Anatolia, nor is the Anatolian population uniform in this respect, although the greenish ground colour unh may occur more frequently in C Anatolia than elsewhere. The few specimens examined from Iran cannot be decisive for a subspecific distinction of the Anatolian population. The form *lecerfi* Verity, 1928 (= *reverdini* Le Cerf, 1914), described from Iran (Bazouft and Lagherit) appears to be an extreme variation with very well-developed and sharply contrasting spots uph (even with white basal spots). I have not seen such extreme specimens, but some specimens from Turkey (near Ankara) resemble these.

Pyrgus armoricanus philonides Hemming

Hemming, 1931 — Ann. Mag. Nat. Hist. (10) 8: 534—535.

Type-locality: Khan Ghaffa (Lebanon).

Material examined. — 5 ♂ Lebanon (BM).

Distribution. — Confined to the Lebanon.

Subspecific characters. — Small, ♂ 11.6—12.7 mm. Differs from ssp. *persicus* mainly in the pale yellowish ground colour unh. Ssp. *philonides* is a little differentiated form in comparison with the great variability of *persicus*.

Note. — According to Hemming (1931: 535): "The genitalia have been examined and differ in no way from nominotypical *armoricanus*." The genitalia of four males (incl. two paratypes) of ssp. *philonides* examined by me turned out to be of the *persicus* type.

Geographic history. — Undoubtedly the *armoricanus* and the *persicus* subspecies groups arose in a West Mediterranean and an East Mediterranean glacial refugium respectively. There is no reason to suppose that the present differentiation within these groups is older than of postglacial age. The two subspecies groups may have originated during the Last Glacial.

The northern localities of this warmth-loving species (Denmark, S Sweden) seem to be relics of a wider distribution in a postglacial period which was warmer than the present (the Atlantic climatic optimum?). If ssp. *disjunctus* is not a nongenetic ecophenotypic variety, a recent colonization of Denmark and S Sweden from N Germany

can also be taken into account, or else a long-lasting similar selection pressure in Denmark and C Germany can have brought about the characters of ssp. *disjunctus* (in this case *disjunctus* cannot be regarded as a subspecies).

In the Balkans the two subspecies groups evidently met postglacially. The fact that the *armoricanus* type of genitalia has been found in Turkey and N Iran does not necessitate the assumption of any other contact between the groups (cf. Alberti, 1940), as this may be a part of the normal variation of the *persicus* group.

18. *Pyrgus alveus* Hübner

Hübner, 1803 — Samml. Eur. Schmett., 1: 70; pl. 92 figs 461—463.

Type-locality: Germany (Verity, 1940).

Distribution (Map 16). — Palaearctic. From NW Africa and Spain to the Amur region. In Scandinavia north to approximately 63° N Lat. The northern limit further eastward is not known. The records of *Pyrgus serratulae* from Vologda and Kotlas (European Russia) by Krulikowsky (1909) presumably refer to *P. alveus*. The same may be the case with the record of *P. serratulae* from the River Vilui (NE Siberia) by Herz (1898). The distribution in W Europe is rather well known. Detailed distribution maps can be found in Agenjo (1963 - Spain), and Nordström, Opheim & Valle (1955 - Scandinavia). *P. alveus* has a restricted range in Peninsular Italy, viz. the larger mountain massives of Marche and Abruzzi (as *P. serratulae* and *P. bellieri*) (Verity, 1940).

In E Europe presumably widely distributed, but many records are unreliable as they may be based on misidentifications. In Asia possibly continuously distributed through Siberia to Vladivostok. In China only found in the Kuku-Nor region, Szechwan and SE Tibet (see below, Material examined).

Rare in warm or lowland districts.

Habitat. — Flowery meadows, waysides, often in large numbers in damp places, e.g. on muddy shores along streams. Most common in hilly and mountainous districts. In the Alps up to 2700 m (Warren, 1928; Verity, 1940), in Szechwan and SE Tibet still found at 4700 m (BM), but also just above sea level, e.g. in N France (Picard, 1948d) and the northern part of E Germany (Urbahn, 1939; Friese, 1956).

Biology. — Monovoltine, but bivoltine in some warm and low localities in the southern Alps (Kauffmann, 1948). It may even produce a second generation at high altitudes (2200 m) in extremely hot years (Warren, 1953); other records of a second generation are unreliable, as confusion with *P. armoricanus* cannot be excluded. The flight period usually is in July and August, but particularly for the *accretus* subspecies group (SW and W Europe) the emergence may begin at the end of May. Kauffmann (1953) recorded *accretus* from SW Germany from the end of May to the end of June, and the specimens I saw from N France mainly date from the end of May to the middle of June. From W France (Charente) I also saw specimens from September which may indicate a second generation.

According to Higgins & Riley (1970) in NW Africa there are two broods a year, but neither Warren (1953) nor I have found any indication for a second generation of *P. alveus* (ssp. *numidus*) in NW Africa. The specimens examined dated mainly from the end of May (25.V) until the middle of July.

Various food plants have been recorded, but reliable records are rather scarce. Most

frequently various species of *Helianthemum* (Cistaceae) and *Potentilla* (Rosaceae) have been mentioned, Rehfoos (*in* Reverdin, 1912) and Kauffmann (1948) observed depositing of eggs on *Helianthemum*, Bergmann (1952) on *Potentilla*; in addition, the last person recorded *Polygala* (Polygalaceae) and *Agrimonia* (Rosaceae) as food plants.

Geographic variation. — An important part of the geographic variation has been outlined in Chapter 2.b, but it will be now discussed in more detail. *P. alveus* has the most variable male genitalia of all Palaearctic species of *Pyrgus*. This variation is partly geographic, partly individual. It is particularly apparent in the development of the cuiller, but also other parts are affected; style, stylifer, antistyle, uncus and lateral apophyses. I will only mention the most obvious variations. The geographic variation in the genitalia is partly connected with a geographic variation in the facies, but generally there is a large individual variation in the facies, presumably due to a high sensitivity to differences in temperature and moisture. Kauffmann (1954c) recorded a breeding experiment that indicated that pupae of *P. alveus* are very sensitive to frost: pupae exposed to temperatures below 0° C produced butterflies which were above totally black. This is of course important for the evaluation of the observed variability.

The geographic variation may be described as follows.

Pyrgus alveus numidus Oberthür

Pl. 6 Fig. 91, 100

Oberthür, 1910 — Ét. Lép. Comp. 4: 404; pl. 50 figs. 484—486.

Type-locality: Algeria.

Material examined. — 130 ♂ 33 ♀ : 78 ♂ 9 ♀ Morocco (Azrou, Daïet-Achlef, Timhadit, Ifrane, Assila, Djebel Hebbri, Bekrit, Tarzeft, Sidi Ali, Anngour) (BM, MP, RJ), 52 ♂ 24 ♀ Algeria (Lambèse, Djebel Aurès, Batna) (BM).

Distribution. — Confined to NW Africa.

Subspecific characters. — ♂ genitalia: cuiller high and narrow, apex rising well above the dorsal ridge of the harpe; harpe of a more or less even width throughout. Facies: a very conspicuously spotted form, also uph. Central spot unh usually with a projection towards the base of the wing and towards the termen along vein 6, absent in 10 % of the specimens examined. Size: ♂ 13.8—15.6 mm.

Variation. — I could not establish a difference between the Moroccan and the Algerian specimens.

accretus subspecies group

The cuiller in specimens from W and SW Europe is characterized by the short free part of the proximal edge of the cuiller, which is one quarter or less of the total depth of the proximal edge and sloping towards the harpe, sometimes almost touching it. The shape of the cuiller is also characteristic, varying from the *alveus* type to the *bellieri* type (see Chapter 2.b).

Some Pyrenean specimens are nearly (?entirely) indistinguishable from *P. bellieri* in the shape of the cuiller. It may be recalled that there are indications in the southern Alps of a rare hybridization between *P. bellieri* and *P. alveus accretus*. Specimens with a less developed cuiller can always be distinguished from ssp. *alveus* by the proximal slant of the free part of the proximal edge of the cuiller, but as stated in Chapter 2.b

specimens have been found in the French Alps which are intermediate between ssp. *accretus* and ssp. *alveus* (also in other characters). The ventral part of the lateral apophyses is rather small in comparison with the type found in ssp. *alveus*, and shorter than the shaft which connects it with the dorsal part.

In the northwestern part of the range (NE France/SW Germany) ssp. *accretus* possibly emerges much earlier than ssp. *alveus* in the adjacent regions (cf. Kauffmann, 1953; see also above, under Biology). The situation in SE France is not very well known, but at any rate the flight periods of ssp. *accretus* and ssp. *alveus* overlap.

The taxonomic position of the *accretus* group is still uncertain. Warren (1953) gave it specific rank, as mentioned in Chapter 2.b. If one gives the *accretus* group specific rank, it is reasonable to consider *numidus* also specifically distinct from ssp. *alveus*, as the differences with ssp. *alveus* are as obvious as between ssp. *accretus* and ssp. *alveus*. For the time being the classification proposed here seems to be practical for the present zoogeographic study.

Agenjo (1963) described the variation in the cuiller in the *accretus* group and part of the *alveus* group as clinal, particularly the variation in the direction of the proximal edge. He based his conclusion on photographs of the genitalia of males from Bavaria, the French Alps, the Pyrenees and C Spain. If he had also presented a picture of the genitalia of a Scandinavian male, the variation would have been still more obvious, but it is not correct to study clinal variation on a selection of individual specimens. Actually, the *alveus* type is, at least in the character mentioned, rather constant throughout C Europe and the *accretus* type is rather constant throughout France and a large part of Spain. This does not suggest a gradual change of the character mentioned by Agenjo.

Within the *accretus* group nine "races" have been distinguished but as some appear ecophenotypic variations or are difficult to define geographically, I will reduce the number of subspecies to four and perhaps even this number should be reduced.

Pyrgus alveus insigniamiscens Verity

Pl. 6 Fig. 92, 101

Verity, 1929 — Trab. Mus. Cienc. nat. Barcelona 11: 14.

Type-locality: Sierra Nevada.

Material examined. — 2 ♂ 2 ♀ : 2 ♂ 1 ♀ Sierra Nevada (BM, RJ), 1 ♀ Sierra de Alfacar (BM).

Distribution. — Only known from the Sierra Nevada and the adjacent Sierra de Alfacar.

Subspecific characters. — Large, ♂ 15—15.6 mm, ♀ 15.7—17.1 mm. Externally almost indistinguishable from ssp. *numidus*, particularly unh. In the male genitalia, however, the free proximal edge of the high and rather narrow cuiller slopes distinctly towards the harpe.

Pyrgus alveus centralhispaniae Verity

Verity, 1925 — Ent. Rec. 37: 56.

Type-locality: C Spain (Montes Universales).

Material examined. — 8 ♂ 6 ♀ : 3 ♂ 3 ♀ New Castille (BM), 3 ♀ Old Castille (BM), 5 ♂ Aragon (Albarracin, Tragacete) (BM, RJ).

Distribution. — C Spain.

Subspecific characters. — Male genitalia: free proximal edge of the cuiller usually closer to the harpe than in any form other than ssp. *insigniamiscens*. Above usually very conspicuously spotted, also uph. Below resembling the Spanish form of *Pyrgus carthami*, but varying towards ssp. *accretus*.

***Pyrgus alveus accretus* Verity**

Pl. 6 Fig. 93—94, 102—103

Verity, 1925 — Ent. Rec. 37: 55.

Type-locality: Gèdre (Hautes Pyrénées).

Material examined. — 317 ♂ 91 ♀: 7 ♂ 2 ♀ Asturias (BM, RJ), 34 ♂ 1 ♀ Spanish Pyrenees - prov. Huesca (ZMA, RJ), 63 ♂ 22 ♀ Spanish Pyrenees - prov. Gerona (BM, MP, ZMA, HC, RJ), 13 ♂ Andorra (BM, ZMA), 1 ♂ 1 ♀ Basses Pyrénées (RJ), 95 ♂ 29 ♀ Hautes Pyrénées (BM, MP, ZMA, RJ), 2 ♂ Ariège (MP, RJ), 54 ♂ 12 ♀ Pyrénées Orientales (BM, MP, ZMA), 1 ♂ Aude (ZMA), 1 ♂ 1 ♀ Hérault, 1 ♀ Gers, 3 ♂ Aveyron, 1 ♂ Charente Mar., 5 ♂ 2 ♀ Charente (all BM), 2 ♂ 2 ♀ Puy-de-Dôme (MP), 8 ♂ 4 ♀ Haute-Loire (BM), 1 ♂ 1 ♀ Loire (BM), 2 ♂ 1 ♀ Saône-et-Loire (BM, RJ), 12 ♂ 8 ♀ Seine-et-Oise (BM, MP), 6 ♂ 4 ♀ Eure (BM), 8 ♂ Alpes Mar. (BM).

I examined the genitalia of 75 males from the Pyrenees and of 25 males from C and N France. A reliable identification of specimens from the French Alps is only possible by a genital examination. Therefore, I have enumerated only the specimens from the French Alps of which I could examine the male genitalia of this subspecies as well as of ssp. *alveus*.

Distribution. — From N Spain to N France and SW Germany. The eastern limit is not exactly known, but ssp. *accretus* seems to be absent east of the Rhine and of the Swiss Jura. According to Warren (1953) populations in NW Italy, in the Cottian and in the Ligurian Alps should also be referred to this subspecies.

Subspecific characters. — With regard to the male genitalia ssp. *accretus* differs from ssp. *insigniamiscens* and ssp. *centralhispaniae* in the free proximal edge of the cuiller usually being less close to the harpe. Some specimens, however, are indistinguishable from ssp. *centralhispaniae* in this respect, e.g. a male from Aude.

Usually less spotted than the two subspecies just mentioned, but there is much variation. For difference with ssp. *jurassicus*, see below.

Variation. — In the Pyrenees there is much variation in size (♂ 13—15 mm), in spotting above and below and in ground colour unh (bright yellow to greenish yellow). The variation is continuous and certainly not geographically defined. Therefore, I consider the distinction of *pyreneialpium* and *necaccreta*, both described by Verity (1929), superfluous and their denomination as subspecies unjustified. A form living in the departments Eure and Seine-et-Oise has been named *lutetianus* by Picard (1948d), mainly differing from ssp. *accretus* in the larger spots and the stronger superscaling with light scales on the upperside (Pl. 6 Fig. 94). However, the only difference I could establish is the absence of darker specimens in the north, which may be due to the absence of high mountains. Many Pyrenean specimens cannot be separated from specimens from N France.

Specimens with very strong light suffusion above and with a pale yellow ground

colour unh from the department Gard have been named *subdecoloratus* by Picard (in Gaillard, 1952). Presumably it is an extreme variation, due to some particular ecological conditions.

Large specimens from the French Alps have been distinguished by Verity (1925) as *grandis*.

In the Pyrenees there exists much variation in the male genitalia. Some specimens may be nearly or entirely indistinguishable from *P. bellieri*. Agenjo even distinguished the subspecies *bellieri hospitalis* from Gerona. I could not find the original description, but Agenjo (1963) used this name for his figure 1 (male genitalia) on plate 2. I have seen comparable genitalia in four males taken in the eastern Pyrenees and in one male taken on the Col du Pourtalet (Basses Pyrénées). For the present it seems advisable to consider such specimens extreme variations of ssp. *accretus*, instead of representatives of western populations of *P. bellieri*. The localities of *P. bellieri* nearest to the eastern Pyrenees are in the south of the department Aveyron, more than 100 miles away.

Pyrgus alveus jurassicus Warren

Warren, 1926 — Trans. Ent. Soc. Lond. 74: 121; pl. 42 figs. 9—12.

Type-locality: Jura.

Material examined. — 3 ♂ 4 ♀: 1 ♀ Weissenstein (Swiss Jura), 3 ♂ 3 ♀ Eclépens (Vaud) (BM).

Distribution. — French and Swiss Jura; Mont Salève (cf. Warren, 1953).

Subspecific characters. — Differs from ssp. *accretus* mainly in being smaller (♂ to about 13 mm) and in having very prominent nervures unh which are outlined in bright yellow-orange. The subspecies is somewhat intermediate between ssp. *accretus* and ssp. *alveus* externally; the male genitalia are typically *accretus*.

As it has a rather large distribution it may be more than an ecophenotypic variation, as e.g. *subdecoloratus*. I did not see enough specimens to get a good impression of the variation.

alveus subspecies group

From C Europe to China the cuiller is characterized by its free proximal edge which is about one third the total depth of the proximal edge (varying to nearly one quarter) and, with slight variation, is directed vertically to the ventral plane of the cuiller. The ventral part of the apophyses is longer than the shaft. The apex of the cuiller is almost level with the dorsal edge of the harpe, but in some specimens it rises well above this edge.

There is very much individual variation in the male genitalia, particularly in the shape of the cuiller. The variation is partly geographically defined. This has been shown by Kauffmann (1954a) in a nice study on the variation in the southern Alps. Using characters of 300 male genitalia he demonstrated that the percentage of specimens with a deformed cuiller (usually a restriction in the horizontal depth) increases from nearly 50 % in the Central Alps to more than 80 % in the pre-alpine zone in the lowlands. In the same way the proportion of specimens with a concavity in the proximal edge of the stylifer (once thought to be a characteristic of the Chinese *reverdini*, see Reverdin, 1916, and Warren, 1952) increases from about 50 % to nearly 90 %. Unfortunately,

Kauffmann compared his rich material from the southern Alps with five males from N Turkestan (Ili), from where Reverdin (1912) described the "subspecies" *iliensis*. As he found a good resemblance between *iliensis* and the lowland *alveus* of the southern Alps, he concluded that they were conspecific and specifically distinct from *alveus*, and named "*iliensis*" of the southern Alps ssp. *columnus*. This is quite incomprehensible, as *alveus* and *columnus*, in this way distinguished, imperceptibly pass into each other in the southern Alps. Moreover, five males from Turkestan are entirely insufficient for a reliable impression of the local variation. Both types of genitalia, with transitions, occur throughout the Central Alps, as correctly stated by Warren (1957) and as can be seen from the fifty-fifty proportion given by Kauffmann himself. Both types also occur in S Bavaria, C Italy and the Balkans in varying proportions. Thus, it is even impossible to define *columnus* geographically. Perhaps a statistical study on much more material from E Europe and Asia than available at present, would give interesting results. At the moment we can only conclude that the *columnus* type predominates in some areas.

This variable *alveus* type of genitalia is widely distributed in Asia. I have stated this type in specimens from the Ili region (Boro Choro), the Altai, Abakan (north of the Altai), the Kuku-Nor region and W Szechwan and SE Tibet. The photographs by Reverdin (1912; pl. 18 fig. 1; the same has been reproduced by Warren, 1926; pl. 9 fig. 5) and by Kauffmann (1954a; pl. 2 fig. 7 and 8), representing *iliensis* from the Ili region, also show the *alveus* type of genitalia. However, the *alveus* type is accompanied in all these regions by the *scandinavicus* type (cuiller dorsally more developed than ventrally, free proximal edge sloping away from the harpe, broad stylifer and antistyle). This is most evident in the Altai and north of it (from W Siberia I saw only the *scandinavicus* type). In the Kuku-Nor region and further south it may be due to intergradation with ssp. *speyeri*. It is impossible to define exactly the geographic boundary between the *scandinavicus* and the *alveus* types in Asia, at least so long we do not have hundreds of specimens available from Siberia; and even then it may be impossible. Provisionally I shall list all Asiatic forms, except *speyeri*, in the *alveus* subspecies group. The male genitalia are in spite of their variability much more constant than the facies, and while it is difficult or impossible to define the variation in the male genitalia geographically, the variation in the facies can, at least in part, be geographically defined. It may be recalled that the species is very susceptible to temperature influences, low temperatures causing a reduction of the white spots above. Knowing this, it is difficult to define subspecies on the basis of external characters, but the following classification may be useful.

Pyrgus alveus alveus Hübner

Pl. 6 Fig. 95—96, 104—105

Material examined. — 554 ♂ 190 ♀: 4 ♂ Alpes Maritimes (MP), 31 ♂ 28 ♀ Basses Alpes (BM, ZMA), 31 ♂ 9 ♀ Hautes Alpes (BM, MP, RJ), 38 ♂ 13 ♀ Savoie (BM), 24 ♂ Haute Savoie (BM), 134 ♂ 37 ♀ Italian Alps (BM, ML, ZMA, RJ), 123 ♂ 64 ♀ Switzerland (Vaud, Valais, Ticino, Berne, Uri, Unterwalden, Grisons) (BM, ML, ZMA, RJ), 23 ♂ 13 ♀ W Germany (Baden-Württemberg, Bavaria) (ML, RJ), 67 ♂ 12 ♀ Austria (N Tyrol, Gross Glockner, Carinthia, Styria Inf.) (BM, ML, ZMA, HC, RJ), 12 ♂ 5 ♀ Hungary (BM, ML, ZMA), 4 ♂ 1 ♀

Rumania (BM, ML, MW), 10 ♂ 2 ♀ Bulgaria (BM), 31 ♂ 4 ♀ Yugoslavia (Bosnia, Herzegovina, Serbia, Macedonia) (BM, ML, ZMA, ZSM, RJ), 5 ♂ Albania (BM, MW), 7 ♂ Caucasus (MP, BA, RJ), 9 ♂ 2 ♀ Transcaucasia (BM, MP, ZMHB), 1 ♂ Hyrcania (BM).

I examined the male genitalia of specimens from the various regions in the following numbers: Alpes Mar. 4, Basses Alpes 16, Hautes Alpes 14, Savoie 12, Haute Savoie 10, Italian Alps 37, Switzerland 25, Germany 15, Austria 22, Rumania 3, Yugoslavia 26, Albania 4, Caucasus 7, Transcaucasia 6, N Iran 1.

Distribution. — C, E and SE Europe, Caucasus to N Iran. The distribution in Russia north of the Caucasus is entirely unknown.

Subspecific characters. — Very variable; not every specimen can be distinguished from specimens of other subspecies of the group (particularly from specimens of *centralitaliae* and *sifanicus*). See the following paragraph.

Variation. — (1). C Europe. Some authors have given subspecific rank to forms which are regarded here as individual or ecophenotypic variations. Apart from *columnus* (see above), these are:

(a). *alticolus* Rebel, 1910 (Pl. 6 Fig. 96, 105). Small, but larger than *Pyrgus warrenensis*, with reduced spots. A form of high altitude, usually flying with larger and more distinctly spotted specimens. There is a confusing synonymy about this form. Evans (1949) used the name for specimens belonging to *Pyrgus warrenensis*, which latter name he regarded as a synonym of *alveus*. Other names used for this form are *ryffelenensis* Oberthür, 1910, and *scandinavicus* Strand, 1903, cf. Warren (1953).

(b). *claralveus* Verity, 1934. Characterized by rather conspicuous and sharp markings uph; ground colour unh greenish or greenish-yellowish, not dark. According to Kauffmann (1951), this form is more common at low than at high altitudes, just as can be excepted from a well-marked form.

(c). *prabornius* Kauffmann, 1951. Above black, with small spots upf and inconspicuous white streaks uph; unh very pale; unh ground colour rather homogenous pale yellow, spots large and coherent; of average size, ♂ 13—13.7 mm. This is, briefly, the original description of *prabornius*. Kauffmann states that it occurs in the "Oberes Nikolaital" in Valais. I have seen such specimens also from other localities, particularly the Gross Glockner region.

(2). SE Europe. Warren (1926) proposed the name *trebevicensis* to replace *reverdini* Schawerda, 1918, the latter being a homonym of *reverdini* Oberthür, 1912 (see below). However, Warren had not seen specimens of this form and relied entirely on the original description of Schawerda and the statement by Reverdin that it is a very striking variety. I do not know whether Warren saw this form in 1952, but at that time he stated that it occurs "from Turin to the Altai Mountains, and the Carpathians to Macedonia" (p. 95). The original description reads (Schawerda, 1918: 23): "Etwas grösser, oberseits heller braun, nicht so dunkel wie die Nennform, normal stark weiss gefleckt. Unterseits sind die weissen Flecke grösser, das Braun lichter, Breitere Flügelform. Flügelspannung meist 29 mm. 5 ♂, 2 ♀, Trebevic, Vucijabara. Von mir im Juli 1907 und 1912 erbeutet." This has little value, in view of the great variability of *ssp. alveus* and, indeed, I have not found any reason to separate Yugoslavian specimens subspecifically from specimens from elsewhere within the range of *ssp. alveus*, as outlined above. By giving *trebevicensis* the rank of subspecies one would reduce the nominate form almost to the rank of an aberration.

(3). Caucasus - Transcaucasia - N Iran. The populations of this region have long been known under the name of *sifanicus*, originally given to Chinese specimens, on account of the white borders unf and unh and the large spots unh in the few specimens known (mainly from Transcaucasia). However, Alberti (1967, 1969) showed by his own captures that the usual form of the Caucasus is indistinguishable from specimens from S Germany. Indeed, six males taken in the Caucasus and sent to me by Alberti appeared to be similar to specimens from S Germany. I saw only one specimen from the Caucasus (Kuban district, MP) with *sifanicus* characters. South of the Caucasus there appear to be proportionally more specimens of the *sifanicus* type. Alberti (1967) found among seven males and five females, five males of the *alveus* type and among the material examined by me (9 ♂ 2 ♀) there were also five males of the *alveus* type, the other specimens resembled in varying degrees ssp. *sifanicus*. The single specimen from N Iran ("Hyrcania") is small (12.6 mm), but otherwise like ssp. *sifanicus*. It is possible that there exists a genetic-historical relation between the Transcaucasian population and the Chinese ssp. *sifanicus*. As a subspecies is a population (or a group of populations) and not a character, it seems at present desirable to refer the populations of the whole region, from the Caucasus to N Iran, to ssp. *alveus*, of course without forgetting the variation in this region.

I have found white borders at the underside also (rarely) in ssp. *numidus*, in the *accretus* subspecies group and (very rarely) in Central European ssp. *alveus*.

Pyrgus alveus centralitaliae Verity

Verity, 1920 — Ent. Rec. 32: 4.

Type-locality: Sibillini Mts.

Material examined. — 74 ♂ 28 ♀ C Italy (Marche, Sibillini Mts.) (BM, RJ).

Distribution. — Confined to C Italy.

Subspecific characters. — Usually small, ♂ 13—14 mm, but as noted by Verity (1940), sometimes reaching 17 mm. Verity believes that the larger specimens are the result of humid weather. Many specimens have clear white markings uph, but as far as I could ascertain, they do not dominate. Ground colour unh usually yellower than in ssp. *alveus*.

Pyrgus alveus iliensis Reverdin

Reverdin, 1912 — Bull. Soc. Lép. Genève 2: 155—157; pl. 16 figs. 7—8; pl. 18 figs. 1—2.

Type-locality: Ili region.

Material examined. — 16 ♂ 8 ♀: 1 ♂ 1 ♀ Kansk (W Siberia) (BM), 1 ♂ Boro Choro (BM), 3 ♂ Abakan (MO), 11 ♂ 7 ♀ Altai (BM, ML). I examined the genitalia of all males, except six from the Altai.

Distribution. — W Siberia to the Altai and the Ili region.

Subspecific characters. — Characterized by the very large and square spots above. This appears to be the usual form of the Ili region (original description; Alberti, in litt.). The specimens from Kansk and Boro Choro agree very well with it. The other specimens have smaller spots, but they are better spotted than most European specimens of ssp. *alveus*. The size varies from 12.4 to 14.4 mm.

Note. — The union of all populations from the Ili region and W Siberia into a single subspecies is provisional, as is the place in the *alveus* subspecies group. As mentioned above, the *scandinavicus* type of genitalia also occurs in this region. I found it in a specimen from Kansk, one from the Altai and two from Abakan.

***Pyrgus alveus sifanicus* Groum-Grshimailo**

Pl. 6 Fig. 97, 106

Groum-Grshimailo, 1891 — Hor. Soc. Ent. Ross. 25: 459.

Type-locality: Kuku-Nor.

Material examined. — 9 ♂ 1 ♀ Kuku-Nor region (Kuku-Nor, Amdo, Sining) (BM, ZMHB). I examined the genitalia of four males.

Distribution. — Only known from the Kuku-Nor region.

Subspecific characters. — Typically distinguished by the white borders unf and unh. However, four males out of nine examined were nearly indistinguishable from European *alveus*.

Note. — (1). A male in the BM, labelled "E Siberia", is externally and on account of the genitalia a typical *sifanicus*. Unfortunately, the locality is rather vague.

(2). The male genitalia are very suggestive of European *alveus*, those in one specimen being indistinguishable from the European structure, the others having the proximal edge of the cuiller rather oblique and the apex of the cuiller more or less massive, in the manner of ssp. *speyeri*.

***Pyrgus alveus reverdini* Oberthür**

Pl. 6 Fig. 98, 107

Oberthür, 1912 — Ét. Lép. Comp. 6: 72, pl. 137 fig. 1217.

Type-locality: Ta-Tsien-Lou (Szechwan).

Material examined. — 20 ♂ 4 ♀: 14 ♂ 2 ♀ Ta-Tsien-Lou, 2 ♂ Chengmengka, 1 ♂ Ying-kuan-chiai, 1 ♀ Kwan-chiai (all Szechwan), 1 ♂ Shiuden Gompa (SE Tibet). 2 ♂ 1 ♀ How Kow (SE Tibet) (all BM). I examined the genitalia of four males.

Distribution. — SE Tibet and W Szechwan.

Subspecific characters. — Above very much like ssp. *speyeri* but spots never as reduced as sometimes in that form. Unh white spots very extended and with a conspicuous white band along termen. Ground colour unh of a particular yellow-green tinge. Central spot unh usually with a projection towards the base of the wing and towards the termen along vein 6.

Note. — (1). Of the male genitalia examined none has the shape of the genitalia figured by Warren (1926; pl. 6 fig. 2). They are suggestive of ssp. *sifanicus* and of ssp. *alveus*. Undoubtedly the male genitalia of ssp. *reverdini* are rather variable, as in all subspecies of *P. alveus*.

(2). Ssp. *reverdini* is possibly confined to very high altitudes. It has been taken from 10,000 ft (How Kow) to 14,000 ft (Shiuden Gompa), but the specimens from Ta-Tsien-Lou lack exact data.

There remain two subspecies to be discussed, viz. ssp. *scandinavicus* and ssp. *speyeri*. I have left them out of the *alveus* subspecies group because their male genitalia are somewhat different. As stated above, there may exist a large-scale intergradation in W Siberia (between ssp. *scandinavicus* and ssp. *iliensis* and possibly even ssp. *alveus*) and in E Siberia and N China (between ssp. *speyeri* and ssp. *sifanicus*). Another interesting region seems N and C Russia, but material is lacking. On the records of

Pyrgus serratulae from Vologda and Kotlas (Krulikowsky, 1909) and of *alveus* with the basal spot in space 7 unh roundish, from Estonia (Petersen, 1924) one may assume that ssp. *scandinavicus* is widespread in N Russia. More material, however, is needed for certainty about this.

The fact that ssp. *scandinavicus* and ssp. *speyeri* are discussed here after the *alveus* subspecies group does not mean that they are more closely related to each other than to that group.

Pyrgus alveus scandinavicus Strand

Strand, 1903 — Arch. Naturv. Christian. 25: 6.

Type-locality: Dovre.

Material examined. — 43 ♂ 10 ♀: 39 ♂ 9 ♀ Norway (BM, MO), 4 ♂ 1 ♀ Sweden (BM, MO). I examined the genitalia of 34 males from Norway and 4 males from Sweden; of 28 ♂ from Norway and 1 ♂ from Sweden I saw only the genitalia.

Distribution. — Norway, Sweden, Finland and possibly N Russia.

Subspecific characters. — Rather small, ♂ 12.4–14.2 mm. Upf spots usually small; they are rather square when they are well-developed. Uph nearly plain brown. Unh spots rather large and sharply contrasting with the deep greyish-yellow or greenish ground colour.

The male genitalia have been discussed above (Chapter 2.b.). In brief it may be recalled that they are characterized by:

(a) broad stylifer and antistyle; (b) dorsally greater development of the cuiller than ventrally; (c) backward slope of the free proximal edge of the cuiller, which is one third to half of the total depth of the proximal edge. The genitalia vary towards the *alveus* type (cf. Opheim, 1956).

Pyrgus alveus speyeri Staudinger

Pl. 6 Fig. 99, 108

Staudinger, 1887 — in Romanoff, Mém. de Lép. 3: 153; pl. 8 fig. 5.

Type-locality: Amur.

Material examined. — 45 ♂ 21 ♀: 1 ♂ E Altai, 1 ♂ 1 ♀ E Sajon, 1 ♂ Irkutsk, 3 ♂ 1 ♀ Kentei Mts., 1 ♀ Viluisk, 1 ♂ 1 ♀ Chita, 16 ♂ 8 ♀ Jablonowyj Khrebet (all BM), 18 ♂ 8 ♀ Amur (BM, ML), 3 ♂ 1 ♀ Little Chingan (BM); 1 ♂ Kuldja (ML). I examined the genitalia of 15 males.

Distribution. — From the E Altai to the Amur region. The male examined from Kuldja (upper course of the Ili River) is a normal *speyeri* without any trace of *iliensis*. If correctly labelled, this specimen may indicate a distributional overlap with *iliensis*.

Subspecific characters. — Externally easily distinguishable by the reduced spots upf which are often partly lost, by the greenish-yellowish superscaling above, by the uniform deep dirty yellow ground colour unh and by the rather reduced spots and the usually roundish or oval basal spot in space 7 unh.

As stated above (Chapter 2.b) the male genitalia are very variable. The cuiller is ventro-distally often flattened, causing a *scandinavicus*-like appearance. The proximal edge of the cuiller is sometimes perpendicular on the ventral line of the valve, but

usually it is distinctly oblique; the free part of the proximal edge is more than one third the total depth of the proximal edge in all specimens examined. The apex of the cuiller is massive and strongly dentate; it usually rises well above the dorsal ridge of the harpe, and in some specimens it is very conspicuous, being highly raised. The harpe is usually rather narrow and of more or less even width.

Geographic history. — A part of the geographic history of *P. alveus* has been outlined in Chapter 2.d, in particular the origin of the subspecies *numidus* and *speyeri* and the *accretus* group. Only additional notes are given here on the *accretus* and *alveus* groups and on ssp. *scandinavicus*.

(a) *accretus* subspecies group. — The differentiation of ssp. *jurassicus* is undoubtedly of a postglacial age as it seems impossible to refer this form to a glacial refugium other than that of ssp. *accretus* (presumably N Spain). The fact that ssp. *accretus* looks more like *Pyrgus bellieri* than ssp. *centralhispaniae* may be due to a contact between ssp. *accretus* (or rather its precursor) and *P. bellieri* during the Third Interglacial. The *bellieri*-like specimens sometimes found in the Pyrenees may be extremes of the *accretus* variation or may indicate a postglacial contact between ssp. *accretus* and *P. bellieri* in the Pyrenees.

During the Last Glacial ssp. *centralhispaniae* apparently originated in a Central Spanish refugial area or at least in an area south of and more or less isolated from where ssp. *accretus* originated.

The glacial history of ssp. *insigniamiscens* (Sierra Nevada) is uncertain, just as its origin. At least its morphologic origin appears rather clear, as its male genitalia seem intermediate between the subspecies *numidus* (NW Africa) and *centralhispaniae* (C Spain).

(b) *alveus* subspecies group. — This may have originated from the form of the Second Interglacial which also gave rise to the precursor of the *accretus* group and to *Pyrgus bellieri* during the Third Glacial. If this is true, the precursor of the *alveus* group must have originated in an eastern refugium during the Third Glacial, but the location of this refugium is obscure (E Europe?, Asia?). The fact that both the Chinese ssp. *sifanicus* and the Transcaucasian *alveus* often have white borders unf and unh may indicate a close relationship. It is not impossible that they are the remnants of an eastern form (the ancestor of the *alveus* group) of the Third Interglacial which have been driven away to border regions. Ssp. *alveus* postglacially largely extended its range from its refugium in SE Europe to the Altai and to the Caucasus region, where it nearly entirely replaced the *sifanicus*-like form in the northern range (the Caucasus proper); ssp. *alveus* replaced that form in the southern range only partially.

The occurrence of a slightly differentiated form in C Italy (ssp. *centralitaliae*) seems to date from a colder period than the present one. Likely, there was a more or less continuous refugial area for ssp. *alveus* during the Last Glacial from Italy to the Balkans. Ssp. *centralitaliae* may be a postglacial geographic isolate of ssp. *alveus*.

The origin of ssp. *iliensis* and its intergradation with other forms must remain obscure as long as the material available from W Siberia and N Turkestan is so extremely scarce.

The geographic origin and history of ssp. *reverdini* is also uncertain. Its distribution suggests that it is an ancient form, but it may also be regarded as a rather recent descendant of ssp. *sifanicus*.

(c) *scandinavicus*. — The *scandinavicus* type of genitalia is found as well in Scandinavia as in W Siberia. It is therefore unlikely that ssp. *scandinavicus* is merely a post-glacial form of ssp. *alveus*. As the greater part (if not the whole) of its present distribution area was covered by land ice during the Last Glacial and as the southern European refugial areas had been taken by other forms (or by their ancestor), ssp. *scandinavicus* must have colonized Scandinavia postglacially from the east (E Russia or W Siberia). Little can be said about the history of ssp. *scandinavicus*, because of the scarcity of specimens available from W Siberia, but the general shape of the cuiller seems to indicate an influence of ssp. *speyeri*. It would not be surprising if ssp. *scandinavicus* turned out to be a hybrid between the subspecies *speyeri* and *alveus* (or *iliensis*). In this connection it is interesting to note that Warren (1953) found a remarkable variation in five out of twenty-seven specimens of ssp. *scandinavicus*, viz. the loss of the apex of the cuiller, "as if a triangular piece had been cut off, from a point half-way down the free edge to one a similar distance from the apex on the dorsal ridge, leaving a straight line connecting two sharp angles." (p. 101).

Indeed, I saw this remarkable form of cuiller in ssp. *scandinavicus* only, but it is impossible to give a percentage of specimens affected, as the cuiller is highly variable. This "lost apex" appears to be the massively sclerotized apex of ssp. *speyeri*.

19. *Pyrgus bellieri* Oberthür

Oberthür, 1910 — Ét. Léop. Comp. 4: 404; pl. 56 fig. 490.

Type-locality: Larche (Basses Alpes).

Distribution (Map 17). — SE France, NW Italy, C Italy. In France it has been taken in the following departments: Aveyron, Lozère, Gard, Ardèche, Drôme, Vaucluse, Bouches-du-Rhône, Var, Alpes Maritimes, Basses Alpes, Hautes Alpes (Picard, 1949b). In N Italy confined to the Cottian and Maritime Alps, in C Italy in the mountains of Emilia, Marche, Abruzzi and Latium (Verity, 1940; Picard, l.c.).

As stated above (under *P. alveus accretus*), some specimens with the *bellieri* type of genitalia have been taken in the Pyrenees, although apparently flying within the range of *Pyrgus alveus accretus* which resembles *P. bellieri* very much. As long as the existence of *P. bellieri* populations in the Pyrenees has not been established, I prefer to regard such *bellieri*-like specimens from the Pyrenees as extreme variations of *Pyrgus alveus accretus*.

Habitat. — Dry, flowery slopes, from 100 to 1700 m (Verity, 1940; Guillaumin, 1964). At Digne (Basses Alpes) I found *P. bellieri* in rather large numbers on mud along a little stream, together with innumerable specimens of the Lycaenid *Lysandra coridon*.

Biology. — Monovoltine; flight period July-August. Larvae and food plants not known.

Geographic variations. — As expected, the geographically isolated C Italian population is somewhat different from the other populations and there is nothing against its separation as a subspecies.

In its restricted range in SE France and NW Italy *bellieri* is rather variable and it has been divided into five "subspecies" by various authors (see Picard, 1949b). I regard them as ecophenotypic variations, as these forms are mainly confined to particular altitudes and very restricted ranges.

Pyrgus bellieri bellieri Oberthür

Material examined. — 221 ♂ 109 ♀: 2 ♂ 2 ♀ Aveyron (BM, ML), 9 ♂ 2 ♀ Lozère (BM), 3 ♂ 2 ♀ Vaucluse (ML), 23 ♂ 6 ♀ Bouches-du-Rhône (BM, ML), 53 ♂ 28 ♀ Var (BM, ML), 24 ♂ 15 ♀ Alpes Maritimes (BM, RJ), 102 ♂ 51 ♀ Basses Alpes (Digne, Larche) (BM, RJ, HC), 5 ♂ 3 ♀ Hautes Alpes (BM).

Distribution. — As that of the species, except C Italy.

Subspecific characters. — A variable subspecies, ♂ 12.5–15.5 mm; usually larger than ssp. *piceus*, with smaller white spots and less strongly white suffusion above. Much variation, however, occurs.

Variation. — Two "races" have been described which are confined to higher altitudes (above 1100 m), viz. *nigropictus* Verity, 1926 (type-locality: Cottian Alps) and *bellieri* Oberthür, 1910 (type-locality: Larche). The latter is characterized by its rather small size, the very strong suffusion of white scales above and the large white spots unh. It occurs as well in the French as in the Italian Alps. According to Picard (1949b) it is the "race" of the highest altitudes. It is the only form recorded from Larche. Some specimens taken at Larche are difficult to distinguish from the lowland f. *foulquieri* and, vice versa, some specimens from the lowlands (Septèmes, St. Zacharie) resemble f. *bellieri* very closely.

The form *nigropictus* is still smaller than f. *bellieri*, above with a rather strong white suffusion, unh with a strong suffusion of dark scales and with smaller white spots than in f. *bellieri*. According to Picard (l.c.) it is confined to the Alps (French and Italian) where it occurs at altitudes higher than 1100 m, but at lower altitudes than f. *bellieri*. Especially the darkened ground colour unh occurs (very infrequently) also elsewhere (Var, Bouches-du-Rhône, Vaucluse).

The other forms, described as races, are: *foulquieri* Oberthür, 1910, *adkini* Picard, 1948, and *gaillardii* Picard, 1948. The last-mentioned form, of which I have seen no specimens, is pale and small and is only known from a few dry and hot localities in Gard and Ardèche.

The form *adkini* is mainly characterized by the very large white spots upf and the bright spots uph. According to Picard (l.c.) it is the race of the "Causses" (Lozère, Aveyron). The specimens I have seen from that region do not allow a subspecific separation.

The form *foulquieri* is variable in size (♂ 12.5–15.5 mm), extension of spots and white suffusion above and extension of spots and ground colour unh. It is difficult (if at all possible) to distinguish this form from the other forms of the subspecies except from extreme f. *bellieri*. Originally *bellieri* and *foulquieri* were described as separate species.

Pyrgus bellieri piceus Verity

Verity, 1920 — Ent. Rec. 32¹: 4.

Type-locality: Sibillini Mts.

Material examined. — 32 ♂ 25 ♀: 26 ♂ 24 ♀ Sibillini Mts. (BM), 1 ♂ Gran Sasso (ML), 3 ♂ Aquila (ZMA), 1 ♂ Sabini Mts, 1 ♂ Roccaraso, 1 ♀ Sorrento (BM).

Distribution. — C Italy.

Subspecific characters. — Small, ♂ 12-14 mm. With regard to the upperside and underside more or less intermediate between the forms *foulquieri* and *bellieri* of subspecies *bellieri*: upf with stronger white suffusion than in f. *foulquieri*, in some specimens as strong as in f. *bellieri*, uph white spots larger than in f. *foulquieri* and unh white spots varying from the size found in f. *foulquieri* to the very broad spots typical of f. *bellieri*.

Geographic history. — As the present morphologic differentiation of *P. bellieri* appears to be of a postglacial age, nothing can be added to what has been said on the history of this species in Chapter 2.d.

20. *Pyrgus warrenensis* Verity

Pl. 4 Fig. 62, 71

Verity, 1928 — Bull. Soc. Ent. France 1928: 140—141.

Type-locality: Lenzerheide (Grisons) (Warren, 1929).

Distribution (Map 18). — Widely distributed in the Alps, but apparently a local species. As far as I know only taken at the following localities: France: Larche, St. Véran, Mt. Cenis, Pralognan (Warren, 1953; Bretherton, 1966; Material examined); Switzerland: Täsch, Zermatt, Ryffel Alps, Lenzerheide (Warren, l.c.; Material examined); Italy: Oulx, Valtournache, Ortler Alps (Warren, l.c.; Material examined); Austria: Samnaun Gruppe, Vent, Brenner Pass, Gross Glockner, Mallnitz (Warren, l.c.; Pröse, 1955b; Material examined); S Germany: Allgäu, Berchtesgadener Alpen (Pröse, l.c.). Many other localities of this high altitude species can undoubtedly be found.

Habitat. — Alpine meadows; presumably not below 1700 m; the upper limit is not known, but specimens have been taken at least at 2500 m.

Biology. — Monovoltine; flight period July—August, according to local conditions. Larvae and food plants not known.

Geographic variation. — Geographic variation has not been established.

Material examined. — 108 ♂ 62 ♀: 37 ♂ 15 ♀ Basses Alpes (Larche), 1 ♂ Savoie, 2 ♂ Mt. Cenis, 5 ♂ 2 ♀ Ryffel Alps, 5 ♂ 2 ♀ Grisons, 3 ♂ Piedmont, 15 ♂ 8 ♀ Valtournache (all BM), 5 ♂ 1 ♀ Ortler Alps (Franzenhöhe), 2 ♂ Ötztal (Vent) (ZMA), 33 ♂ 34 ♀ Gross Glockner (BM, ML, RJ).

Geographic history. — See Chapter 2.d.

21. *Pyrgus jupei* Alberti

Pl. 4 Fig. 63, 72

Alberti, 1967 — Deutsche Ent. Zeitschr. 14: 464—465; pl. 1 figs. 1 a—b; pl. 2 figs. 1 a—d; pl. 3 figs. 2 a—f.

Type-locality: Kasbek (C Caucasus).

Distribution (Map 18). — Caucasus and Transcaucasia. Very few localities are known at present, but undoubtedly *P. jupei* is more widely distributed in this rather poorly explored region.

The localities known at present are: Caucasus: Tschutschur Pass, Kasbek, Karaugom, Passanauri; Transcaucasia: Achalzich, "Chotschalj", Borshom (Alberti, 1967, 1969, in litt.; Material examined).

Habitat. — Alpine meadows, 1700—2700 m.

Biology. — Unknown. Flight period presumably mainly in July.

Geographic variation. — Unknown.

Material examined. — 6 ♂ 1 ♀: 1 ♂ Kasbek (BA), 4 ♂ 1 ♀ Passanauri (BA, RJ), 1 ♂ Borshom (BM).

Geographic history. — See Chapter 2.d.

22. *Pyrgus schansiensis* Reverdin

Reverdin, 1915 — Bull. Soc. Lép. Genève 3: 109—112; pl. 5 fig. 3, pl. 6 fig. 5.

Type-locality: Ta-tsing-schan (Shansi).

Distribution. — Apart from the type-locality only known from Kinschou (Fengtien, Manchuria) (Alberti, 1940) and the Stanovoy Khrebet (RJ).

Habitat, biology and geographic variation. — Unknown. It should be born in mind that the specific rank of *schansiensis* is disputable.

Material examined. — 1 ♂ Stanovoy Khrebet (RJ).

4. DISCUSSION OF SOME ZOOGEOGRAPHIC PROBLEMS

4.a. The geographic origin of species and groups of species

Any attempt to reconstruct the geographic history of a species eventually leads to the question: where did this species come into being. If we define speciation as the process by which a population (or group of populations) acquires reproductive isolation, the geographic origin of a species evidently is the region where the speciation took place, irrespective of subsequent extensions of the range or further differentiation. Matters become complicated when through geographic isolation a further differentiation has led to species multiplication. Virtually one of the new species will resemble the parental species more closely than the other new species and can be regarded as the temporal representative of the parental species. Alberti (1955b) describes this as follows: "Vom theoretischen Grenzfall abgesehen, wird praktisch immer mehr oder weniger lange die Mutterart neben der Tochterart existieren." (p. 218). The problem whether one considers the parental species to have become extinct or still to exist after species multiplication, is mainly of phylogenetic importance (cf. also the discussion on the species in time dimension in Hennig, 1966), but it has also a bearing on the denomination of the geographic origin of a species. If we consider the parental species still to exist after its multiplication, there is no obvious reason to suppose that it still exists in the region where it originated. This region may be populated by what we regard as a new species, instead of the continuation of the parental species. In this case the parental species and the new species have the same geographic origin. If fossils are absent, we can make a distinction between a parental species and a new species only on the basis of a difference in the frequency of characters which are supposed to be primitive, as the parental species must have retained more primitive characters than the new species.

The above considerations also apply to the geographic origin of subspecies (if we define the subspecies as an actually or formerly geographically isolated group of populations, see Chapter 1.b).

In the reconstruction of the geographic history of the *centaureae* species group

(Chapter 2.d) it was supposed that a repeated speciation had taken place in Siberia. This led to the statement, that all three species of the group had a Siberian origin, although two of them (*P. andromedae* and *P. cacaliae*) at present are restricted to European mountains. Of the third species of the group (*P. centaureae*) the European and American subspecies seem to have originated in Siberia, just as the Siberian subspecies did in a more recent time. These considerations led to the statement, that from the phylogenetic point of view the difference between a European and a Siberian origin in cold-adapted species is gradual: it depends on the number of primitive characters, retained in the European and the Siberian populations, respectively. This is only another way of stating that the assignment of a species as parental species depends on the number of supposedly primitive characters, but it shows the bearing of phylogenetic considerations on zoogeographic classifications (see Chapter 5).

With respect to the total distribution area of the *centaureae* group, the distributional areas of *P. andromedae* and *P. cacaliae* are peripheral. In the second part of this chapter it will be shown that the occurrence of primitive characters in peripheral populations does not appear exceptional. It may suffice here to call attention to the possibility that the geographic origin and the present distribution area of a species or subspecies lay far apart.

In systematic studies one can often find such general statements as "genus A-us is of European origin" or "family B-idae is of Palaearctic origin". For example, while discussing the *Pyrgus* group of genera, Evans (1953) stated: "The group is of Palaearctic origin with a considerable development in the Nearctic and Neotropical region" (p. 2).

Evidently the authors of such statements do not bother about the meaning of the expression "the geographic origin of a genus" or of whatever group of species. Unlike the origin of a species, the origin of a genus has no time dimension. Although a genus may be a monophyletic, quite natural group of species, one cannot indicate a moment or period in which the genus became generically distinct from other genera. Virtually a genus originates in the brain of an author, as it is a subjectively delimited group of species. Apparently the brain of an author is not meant by "the geographic origin of a genus". The geographic origin of a group of species can be defined as the region where the differentiation took place which led to this particular group of species. This is a very vague definition, but one should realize that the geographic origin of a group of species is something quite different from the geographic origin of a species.

Possibly some authors mean by the geographic origin of a group of species the geographic origin of the ancestor of the group, whatever this may be. I can understand the statement of Evans mentioned above only in this way. The way a definition reads, is less important, so long a definition is provided.

4.b. The geographic history of the Palaearctic *Pyrgus* species in relation to the general history of the Palaearctic fauna

The occurrence of species and subspecies with primitive characters in border regions, as indicated in the first part of this chapter, appears to be a widespread phenomenon in the Palaearctic fauna. The fact of a character being primitive often is very uncertain. In some cases it is concluded from morphologic data, as in the *centaureae* species group and in superspecies *malvae* (Chapter 3). In other cases it is concluded from the distributional discontinuity of the character, if this character is supposed to have no adaptive

value (e.g. characters of the genitalia). Consequently, the occurrence of primitive characters in border regions (in a broad sense) can be accepted in *Pyrgus* in the following cases:

- (1). The *centaureae* species group. Widely distributed in the colder parts of the Holarctic; primitive characters in European mountains (*P. calcaliae* and *P. andromedae*).
- (2). Superspecies *malvae*. Distributed throughout the greater part of the Palaearctic; most primitive characters in the W Mediterranean region (*P. malvoides*), less primitive characters in the E Mediterranean region (*P. melotis*) and E Asia (*P. malvae kauffmanni*), most recent characters in the intervenient area (*P. malvae malvae*).
- (3). The *alveus* species complex. Distributed throughout the greater part of the Palaearctic; primitive characters still very uncertain, but a possible distribution of such characters can be described as follows: NW Africa (*P. alveus numidus*), Alps (*P. warrenensis*), Caucasus (*P. jupei*) and E Siberia (*P. alveus speyeri*).

It is difficult to trace this phenomenon in the literature concerning other families of Lepidoptera, as this literature usually is merely taxonomic and phylogenetic reflections are left out of consideration. Possibly the following distributional patterns concern the occurrence of primitive characters in border regions:

- (4). *Papilio machaon* (Papilionidae; Eller, 1936—1938) is distributed throughout the Palaearctic; *P. machaon saharae* (NW Africa) and the closely related *P. hospiton* (Corsica and Sardinia) are supposed to be primitive forms.
- (5). The *Melitaea phoebe* group of species (Nymphalidae; Higgins, 1941) is widespread in the Palaearctic; *M. aetherie* (S Spain and NW Africa) and *M. collina* (E Mediterranean) are possibly more primitive than the other species of the group.
- (6). The *Euphydryas aurinia* group of species (Nymphalidae; Higgins, 1950) is widespread in the Palaearctic; *E. desfontainii* (W Mediterranean) and *E. orientalis* (E Mediterranean) may be more primitive than the other species of the group.

In addition, three instances quoted from zoogeographic studies on forest birds are:

- (7). The Woodpeckers of the *Dendrocopos major* group are distributed throughout the Palaearctic. The presumably most primitive members of this group, *D. catapharius* and *D. darjellensis*, are restricted to SE Palaearctic border regions: chiefly the Himalayas to SW China (Voous, 1947).
- (8). The genus *Pyrrhula* (Bullfinches) occurs in the Palaearctic region and in the Oriental region in the Himalayas and to the southeast as far as Formosa, the Philippines and the Malayan peninsula. *P. nipalensis* is considered the most primitive form; it occurs from the W Himalayas to NW Yunnan and in a few isolated ranges further south and southeast (Voous, 1949).
- (9). The Nuthatches of the *Sitta europaea* group, distributed throughout the Palaearctic and part of the Oriental region, are supposed to have descended from the *S. canadensis* group, which has a highly discontinuous distribution: Corsica, Asia Minor and Caucasia, E Asia and N America. *S. canadensis* probably invaded America from E Asia. *S. canadensis yunnanensis* (Yunnan, W Szechwan) is the most conservative of the living forms of the *S. canadensis* group (Voous & van Marle, 1953).

The above instances concern groups with a very wide distribution in the Palaearctic. At least in *Pyrgus* the occurrence in peripheral regions of primitive forms of species or species groups with a restricted range (e.g. European) is not apparent (see also below).

As one would expect to find primitive forms mainly in regions which have remained rather undisturbed by ecological changes since long, it is not surprising that most of the primitive forms mentioned above occur in regions which are known to have been refugia for the Palaearctic fauna of temperate regions during the Pleistocene glaciations (Reinig, 1937; De Lattin, 1951-52, 1967). Evidently the forms, which were most successful in reoccupying regions, which were uninhabitable during glacial times, are the most advanced forms. Species and species groups with a restricted range and without primitive forms in border regions may be primitive themselves, at least when they can be regarded as rather close relatives of species with a Palaearctic distribution. In Chapter 2.d, *Pyrgus cinarae* and *P. armoricanus*, both restricted to the SW Palaearctic, have been considered to be the most primitive members of the *alveus* species complex, which has a Palaearctic range, on the ground of their morphologic characters and habitat preference. On similar grounds *P. carthami* and *P. sidae*, both restricted to the SW Palaearctic, have been considered to be older than the widely distributed *P. centaureae* group. Further there is morphologic evidence for the supposition that the *Pyrgus* species which are restricted to the SE Palaearctic (e.g. *P. maculatus*, *P. oberthuri*) are the most primitive of the Palaearctic *Pyrgus* species.

In conclusion, it appears to be a widespread phenomenon in the Palaearctic fauna that in groups with a Palaearctic distribution the most primitive members have restricted, more or less peripheral ranges. The most important factors leading to this distributional pattern possibly are:

- (1). The Pleistocene glaciations. During glacial periods all species in the Palaearctic, which were not adapted to a cold climate, were confined to refugial regions, situated south of the land ice. These refugia were situated more peripherally than centrally in the Palaearctic.
- (2). Differentiation during geographic isolation. Formerly connected populations could differentiate during geographic isolation in refugia. Some populations retained more primitive characters than others.
- (3). The most advanced forms were most successful in re-occupying lost territories. Possibly the glacial refugia for these forms were situated more closely to the land ice than the refugia of the more primitive forms. This would explain the loss of primitive characters (by high selection pressure) and give the advanced forms a geographically (and perhaps ecologically) favourable starting position for the re-occupation of the Palaearctic.

The particular distributional pattern of primitive and advanced forms in the Palaearctic appears to contradict the statement of Mayr (1963): "the "original" phenotype of a species is usually found in the main body or central part of a species range, while the peripheral populations, particularly the peripherally isolated populations, may deviate secondarily in various ways" (p. 386). Mayr did not take the geographic history of the species into account in this case. In the instances mentioned above the "original" phenotype of the species in the central part of the range has become extinct by the glaciations and the peripheral populations which deviated most from the "original" phenotype, re-occupied the lost territories after the retreat of the land ice. These expanding populations may have attained reproductive isolation with regard to formerly conspecific, at present more primitive populations. In many cases no populations were available for the re-occupation of the Palaearctic in postglacial times, possibly as a result of specialized ecological demands or of the deteriorating effect of the succession of four

glacial periods. In these cases the species are relics in their present, restricted ranges and, of course, the present area of distribution is no indication of the geographic origin.

After this general discussion some aspects of the history of two types of fauna will be treated, as far as it may be useful for the understanding of the history of the *Pyrgus* species.

Cold-adapted fauna. — In his interesting work on the history of the cold-adapted Holarctic fauna, Petersen (1954) pointed to the absence of endemic genera or even subgenera in the Arctic butterfly fauna. He attributed this absence to the great exchange of forms during the Pleistocene between the Arctic and mountains of the temperate zone. Apart from this exchange, the Arctic fauna may be too young for the development of endemic genera. The typical tundra fauna appeared in C Europe first at the end of the long Second Interglacial, although such cold-adapted animals as *Tichorhinus*, *Rangifer* and *Ovibos* have been found as early as the Second Glacial (Petersen, p. 274).

Both the exchange between the Arctic and mountains of the temperate zone and the late appearance of cold-adapted species in Europe are indicated by the distribution and supposed history of the species of the *Pyrgus centaureae* group (*P. centaureae*, *P. cacialiae*, *P. andromedae*). This history has been discussed extensively in Chapters 2.d and 3, and can be summarized here as a series of three invasions from Siberia into Europe. The most ancient invasion, which can be traced at present, took place during the Second Glacial (*P. andromedae*). The *P. centaureae* group has a boreoalpine distribution in Europe; *P. centaureae* is possibly continuously distributed in Asia from the S Siberian mountains (Altai, Sajon) north to the Arctic region. A list of Lepidoptera with a boreoalpine distribution can be found in Warnecke (1959).

The other cold-adapted *Pyrgus* species in Europe, viz. *P. carlinae*, *P. warrenensis* and *P. jupei*, are supposed to have originated during the Pleistocene from more temperate or eurytherm species in Europe. Many cold-adapted species, which are at present restricted to European mountains, may have originated in this way, or else, they may be descendants of such species. Kostrowicki (1969), discussing the Papilionoidea of the European mountains stated that "the tundra species did not take part in the formation of the fauna of the Alpine tiers in European mountains, and species now living in that tier came into being from autochthonous original forms." (p. 207). Although he appears to have overlooked the exchange of cold-adapted species between the European and Asiatic mountains through the Arctic, he may be correct in supposing a European origin for by far the greater part of the cold-adapted species of European mountains. I have not found any indication that these species are older than of Pleistocene age. Warnecke (1958) suggested that the species of the butterfly genus *Erebia* are much older: "During the eocene, with the formation of the last high mountains (especially those of the Alps in Europe), there has obviously been another transformation and evolution of alpine species, for instance those of *Erebia*." (p. 724). More than half of the about 77 species of *Erebia* (Warren, 1936; Higgins & Riley, 1970) are confined to European mountains. Warren classified the *Erebia* species into 14 species groups, of which only one, viz. the *pronoe* group (10 species), is restricted to European mountains. As far as the other groups have representatives in Europe, they have also representatives in Siberian mountains, thus indicating the exchange of forms between European and Asiatic mountains. This exchange has been possible only during the Pleistocene and hence European species belonging to groups with representatives in Siberia possibly originated during the Pleistocene.

As the present European cold-adapted species appear to be of a rather recent, Pleistocene age, the question arises whether there has been a European cold-adapted fauna in the Tertiary. In *Pyrgus* there are no indications of such a fauna. If there have been *Pyrgus* species in the alpine zone of European mountains in the Tertiary, these were probably eurytherm, also occurring at lower altitudes. The present cold-adapted Asiatic *Pyrgus* species, all belonging to the subgenus *Scelotrix*, on the other hand, may be of a Tertiary age or at least, they have retained more primitive characters than the cold-adapted species which originated in Europe (see also Chapter 2.d).

It is improbable that the European alpine fauna in the Tertiary consisted of eurytherm species only. The ancestors of some *Erebia* species groups possibly were cold-adapted European Tertiary species, but indications are still vague. In other genera of butterflies there are no indications of a cold-adapted European fauna in the Tertiary, but in the geometrid genus *Psodos* the Tertiary ancestors of the six species groups, which all except one are limited to European mountains (cf. Petersen, 1954), may have been cold-adapted European species.

Temperate fauna. — Some problems concerning the history of the temperate fauna of two regions, viz. the E Palaearctic and Europe, will be discussed now.

(a). East Palaearctic. The wealth of species, many of which are considered old ("arctotertiary") has tempted some authors to consider this region a centre of origin of a large part of the Eurasiatic fauna (e.g. De Lattin, 1951-52). In my opinion this conception is incorrect. As stated above, a large number of ancient species in a particular region indicates that this region has been little disturbed by ecological changes since long, but can tell us little about the geographic origin of the species. If the preglacial, temperate fauna was rather homogenous throughout the Palaearctic (De Lattin, l.c.), the large number of old, temperate species in the E Palaearctic region indicates the extinction of many species in the W Palaearctic. This extinction appears to have been most important among species living on trees. While discussing the edaphic structure of the species of Papilionoidea in the faunas of the northern Mediterranean coast, Kostrowicki (1969) stated: "The share of species living only on trees and shrubs is insignificant in the above faunas; it is almost identical with the remaining faunas of the province. So the problem arises what happened to the old Tertiary sylvatic fauna, the traces of which are so distinct in the Far East? . . . it may be assumed that the sylvatic Tertiary species became extinct and only those have been preserved which live on herbs (and also ubiquitous species)." (p. 214). As far as known, the *Pyrgus* species live on herbs (and shrubs?) only. If there has been any extinction in the Palaearctic of a part of *Pyrgus*, it has been largely surpassed by differentiation, as there are at present more temperate *Pyrgus* species in the W Palaearctic than in the E Palaearctic. Virtually, only one temperate *Pyrgus* species is restricted to the E Palaearctic, viz. *P. maculatus*. As this may be one of the most ancient Palaearctic *Pyrgus* species, the present distribution is hardly an indication of the geographic origin. So we can only state, that *P. maculatus* has a Palaearctic origin.

(b). Europe. According to Kostrowicki (1969), 372 species of Papilionoidea have been recorded from the region covered by N China, the Amur district, Korea, Sakhalin and Japan; these species, as a whole, have an outstanding temperate character. From the W Palaearctic (west of the Russian frontier and the Bosphorus) 338 species of Papilionoidea have been recorded, of which less than 200 can be called temperate (cf. Higgins & Riley, 1970). Therefore, the number of eight temperate *Pyrgus* species

in Europe (*carthami*, superspecies *malvae*, *onopordi*, semispecies *cirsii*, *serratulae*, *armoricanus*, *alveus* and *bellieri*) appears to be exceptionally large, as there are only three or four temperate *Pyrgus* species in the E Palaearctic (*maculatus*, superspecies *malvae*, *alveus* and possibly, *schansiensis*). The absence of six temperate *Pyrgus* species in the E Palaearctic does not appear to be the result of extinction in that region. Apart from *P. carthami*, these species are supposed to be of a recent, possibly early Pleistocene age. Their thermophilous character may have prevented these species from extending the distributional area far to the east during the Pleistocene. Only species which can live in a cool temperate climate (in *Pyrgus*: *alveus* and superspecies *malvae*), extended their range during the Pleistocene over the western and eastern part of the Palaearctic. *P. carthami*, however, may be an ancient species (cf. Chapter 2.d) and its European origin is not quite certain.

Although the temperate *Pyrgus* species differ much with regard to their habitat preference, it is difficult to make a sharp distinction between warm temperate species of lowlands and rather cool temperate species of mountainous regions, as there is much overlap in the habitats. It is also difficult to make a sharp distinction between warm temperate and Mediterranean species. The thermophilous *P. onopordi*, *P. armoricanus* and *P. cirsii* occur in regions with Mediterranean maquis and steppe vegetation, as well as in less dry regions. There is no objection against their denomination as Mediterranean species, but I prefer to use that term only for species which are mainly or entirely confined to maquis or steppe vegetation. Therefore, of the *Pyrgus* species, only *P. cinarae* and *P. sidae* are termed Mediterranean species here.

All temperate *Pyrgus* species in Europe occur in Spain, except *P. bellieri*, which has a restricted range in Italy and France. However, only three of these species, viz. *P. onopordi*, *P. armoricanus* and *P. alveus*, also occur in NW Africa. This is in accordance with the general view that there was no land bridge over the Mediterranean at any time during the Pleistocene and that mainly flying animals were successful in crossing the Strait of Gibraltar (Moreau, 1955). Evidently the chance of a successful crossing of the Strait of Gibraltar has not been small for butterflies. Of the about 140 non-cold-adapted species of Papilionoidea in Spain, 81 are represented in NW Africa; they outnumber the tropical species in that region largely (cf. Higgins & Riley, 1970). Of the 19 species of Hesperioidea, which occur in NW Africa, only three, (*Gegenes nostrodamus*, *G. pumilio* and *Borbo borbonica*) can be called tropical and nine temperate; the remaining seven can be regarded Mediterranean species.

5. ZOOGEOGRAPHIC CLASSIFICATION OF THE PALAEARCTIC *Pyrgus* SPECIES

Many lepidopterists have been engaged in a zoogeographic classification of Palaearctic (mainly European) species. They have often stated, that a zoogeographic classification must be founded on the present distribution of species alone (e.g. Rebel, 1932; Amsel, 1939; Wiltshire, 1945). This idea has led to the distinction of many distributional types and the division of the Palaearctic region into zoogeographic regions. Recently, Kostrowicki (1965, 1969) divided the Palaearctic area into 43 units (subrealm, province, region, transition zone) on the basis of an analysis of the distribution of the Macrolepidoptera and distinguished 115 "areographic elements and subelements", i.e. distributional types.

As Voous (1963), pointed out this geographic method of classification is a part of

the classic zoogeography of P.L. Sclater and A. R. Wallace. It is a merely descriptive, static method, although often used as a starting point for historical considerations (e.g. Friese, 1958; De Lattin, 1964; Kostrowicki, 1969).

As the present distribution of species is the result of historical events, it is not clear to me, why these events should not be taken into account in a zoogeographic classification. Stegmann (1938) strongly advocated such a dynamic approach. This led him to the recognition of faunal types, instead of faunal regions. His classification was refined by Voous (1960), in his zoogeographic classification of the European birds. I will follow this system in the classification of the Palearctic *Pyrgus* species.

The term "faunal type" refers to the characters of the regional fauna indicated. The characters of a regional fauna result from the particular history of that fauna, its geographic distribution and the habitats afforded in the range covered (Voous, 1960, p. 6). A species can be referred to a particular faunal type, if it, by its origin and history, is a characteristic element of the regional fauna indicated, i.e. if it has taken part in, or has been subjected to, the geographic and climatological history of that fauna.

The Palearctic *Pyrgus* species can be referred to the following faunal types (the descriptions of the faunal types, according to Voous (1960), have been added in parentheses).

Siberian-Canadian (belonging to the fauna of the boreal climatic zone in the Holarctic, notably in the coniferous forest belt) — *P. centaureae*.

Palearctic (belonging to the fauna of the cold, temperate, and subtropical regions of the northern half of the Old World) — *P. maculatus*, *P. malvae*, *P. alveus*.

European (belonging to the fauna of the temperate and Mediterranean regions of Europe) — *P. carthami* (?), *P. malvoides*, *P. serratulae*, *P. onopordi*, *P. cirsii*, *P. armoricanus*, *P. bellieri*.

Mediterranean (belonging to the fauna of the Mediterranean region) — *P. sidae*, *P. cinarae*.

Palaeomontane (belonging to the fauna of the alpine or nival zones of the high mountains of the Palearctic) — *P. badachschanus*, superspecies *P. alpinus*, *P. andromedae*, *P. cacaliae*, *P. carlinae*, *P. warrenensis*, *P. jupei*.

The following notes may be added to this survey.

(1). The species *P. bieti*, *P. oberthuri* and *P. dejeani* cannot be classified zoogeographically, because of lack of data on distribution and habitat preference. Possibly they can be referred to the Tibetan faunal type (belonging to the fauna of the Tibetan highlands in the tundra climatic zone; some members of this group have spread into the alpine zones of central and western Palearctic high mountains).

(2). *P. melotis* cannot be assigned to one of the faunal types proposed by Voous. By its distributional area this species can be called Mediterranean, but with regard to habitat preference only *P. m. melotis* can be assigned to the Mediterranean faunal type.

(3). It is possible that *P. sidae* and *P. cinarae* could better be listed as elements of the palaeo-xeromontane fauna (belonging to the fauna of the arid slopes of the low mountains of the southern Palearctic; some palaeo-xeromontane elements have, after the latest glacial period, spread into the dry, sunny slopes of the high mountains).

The difference between the concept of faunal types and that of distributional types is comparable with the difference between the biological and the typological species

concept: it is the difference between a dynamic and a static approach. This does not in all cases find expression in the denomination, just as the application of the biological species concept does not necessarily result in an other delimitation of the species than the application of the typological species concept.

The distributional types are often explained as the result of the influence of the Last Glacial on the distribution of the Palaearctic species (Fries, 1958; De Lattin, 1964). This gives the distributional types a more dynamic character, but as it only takes the recent history into account, the faunal type and the distributional type, to which a particular species may be assigned, does not need to coincide. This is apparent, if we compare the zoogeographic classification of the *Pyrgus* species given above with a classification based on distributional types. Fries (1958) classified the Rhopalocera (Hesperiidae inclusive) of C Europe into twelve distributional types, to which the C European *Pyrgus* species are assigned as follows:

"boreo-altaisch-alpiner Verbreitungstyp": *P. andromedae*.

"altaisch-alpiner Verbreitungstyp": *P. cacialiae*, *P. cirsii*.

"atlanto-mediterraner Verbreitungstyp": *P. malvoides*, *P. onopordi*, *P. cirsii*.

"ponto-mediterraner Verbreitungstyp": *P. sidae*.

"euromediterran-vorderasiatischer Verbreitungstyp": *P. armoricanus*.

"europäisch-westasiatischer Verbreitungstyp": *P. carthami*.

"euro-asiatischer Verbreitungstyp": *P. malvae*, *P. serratulae*.

"palaearktischer Verbreitungstyp": *P. alveus*.

To the four remaining distributional types ("europäisch, holomediterran, europäisch-vorderasiatisch, circumpolar") no *Pyrgus* species have been assigned.

6. SUMMARY

1. Twenty-two species (including three superspecies) of *Pyrgus* have been recognized in the Palaearctic region.

2. An attempt has been made to distinguish between subspecific, clinal and nongenetic ecophenotypic variation. As a result, many subspecies of earlier authors have been assigned to clinal and ecophenotypic variation.

3. Clinal variation is presumably widespread in *Pyrgus* species, but appears most noticeable in the semispecies *P. cirsii* and *P. carlinae*.

4. Three superspecies have been recognized, viz. *P. alpinus*, *P. malvae* and *P. carlinae*.

5. The dynamic character of the species and the subjective character of the distinction of species is particularly apparent in the *alveus* species complex.

6. An attempt has been made to reconstruct the geographic history of the genus as a whole and that of the separate species. This reconstruction bears clearly evidence of the influence of the Pleistocene glaciations on the distribution and geographic history of the species.

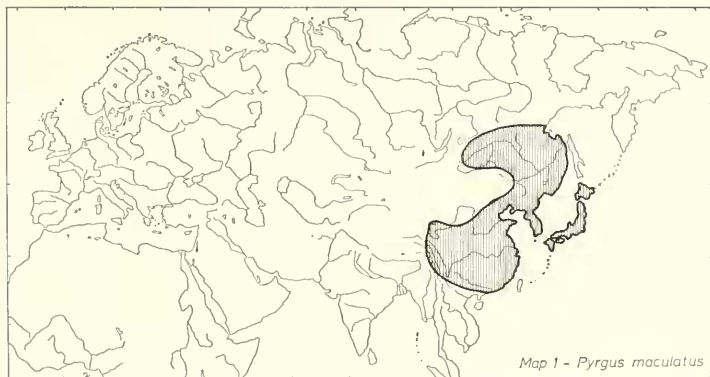
7. On the basis of the supposed history of the *P. centaureae* group of species attention has been drawn to the possibility that the geographic origin and the present distribution of a species lay far apart.

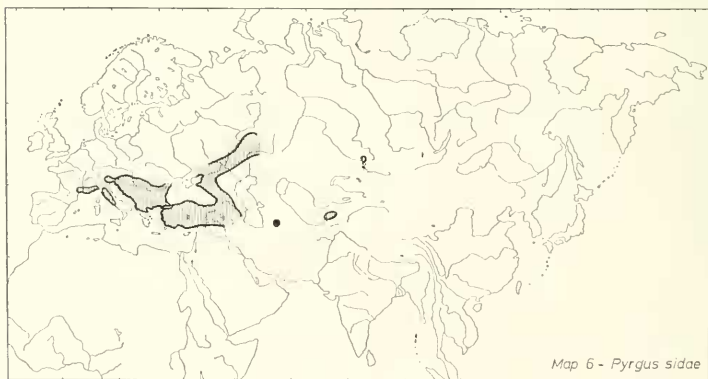
8. The occurrence of primitive forms in Palaearctic border regions has been discussed and a tentative explanation of this distributional pattern has been given.

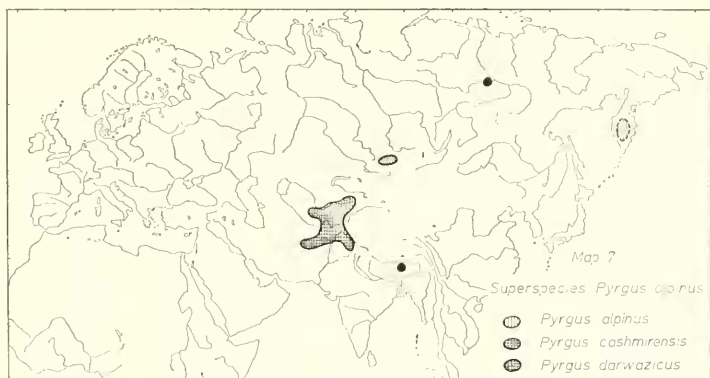
9. The geographic history of the *Pyrgus* species has been discussed in relation to the

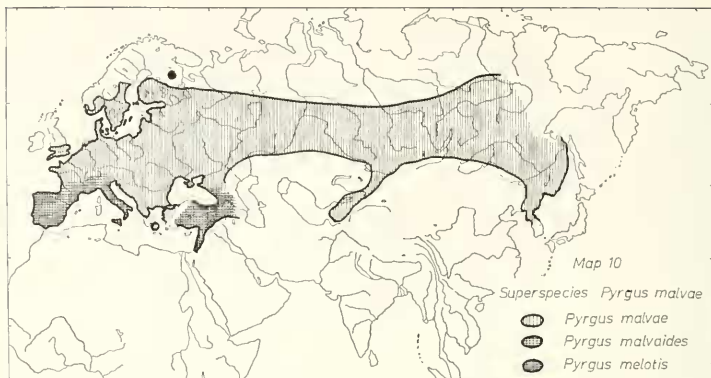
general history of the Palaearctic fauna. *Pyrgus* is noticeable for its relatively large number of temperate species in the W Palaearctic.

10. A zoogeographic classification into faunal types has been applied to the Palaearctic *Pyrgus* species. These species can be assigned to five faunal types. A comparison has been made with the more static method of classification into distributional types.

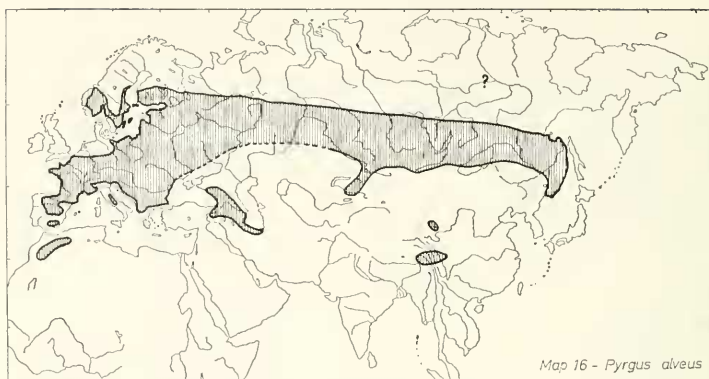












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